PALEONTOLOGY

Volume 28 JANUARY, 1954 Number 1

JOURNAL OF PALEONTOLOGY

UNIVERSITY OF MICHIGAN
FEB 18 1954
MUSEUMS LIBRARY

A publication of The Society of Economic Paleontologists and Mineralogists *and* The Paleontological Society *with the generous support and cooperation of* The American Association of Petroleum Geologists *and* The Geological Society of America

CONTENTS

Faunas and age of the Amsden formation in Wyoming ..... *C. A. Burk* 1
A Permian (Wolfcampian) fauna of the Casper formation of southeastern Wyoming ..... *Selmer L. Pederson* 17
Growth and decline of populations and the distribution of marine pelecypods ..... *David Nicol* 22
Notes on mammals from the Upper Cretaceous Lance formation of Wyoming ..... *Albert E. Wood* and *John B. S. Ormsbee* 26
Primaraucaria, a new araucarian genus from the Virginia Triassic ..... *Wilhelm Bock* 32
Campylocynodon personi, a new Oligocene carnivore from the Beaver Divide, Wyoming ..... *Robert G. Chaffee* 43
A new Lower Cretaceous stromatoporoid, *Bekhemia wetzeli*, from northern Iraq ..... *R. G. S. Hudson* 47
Cambroporella and *Coeloclema*, Lower Cambrian and Ordovician bryozoans ..... *Maxim K. Elias* 52
Internal shell structures in the Middle Cambrian gastropod *Scenella* and the problematic genus *Stenothecoides* ..... *Franco Rasetti* 59
A new *Pseudaelurus* from the lower Snake Creek fauna of Nebraska ..... *J. R. Macdonald* 67
A new Permian crinoid from Western Australia ..... *Curt Teichert* 70
Application of cellulose peel technique to fenestrate sections ..... *John W. Koenig* 76
Trackways of an ambystomid salamander from the Paleocene of Montana ..... *Frank E. Peabody* 79
Distribution of American Pennsylvanian cephalopods ..... *A. G. Unklesbay* 84
Nomenclatural review of genera and subgenera of Cucullaeidae ..... *David Nicol* 96
Some fossorial mammals from the Tertiary of western North America ..... *Charles A. Reed* 102
NOTICES 42, 66, 69
PALEONTOLOGICAL NOTES 112
SOCIETY RECORDS AND ACTIVITIES 120

EDITORS

WILLIAM R. EVITT, for The Paleontological Society.

GROVER E. MURRAY, for The Society of Economic Paleontologists and Mineralogists. Associate editors: W. C. Bell, Dept. Geology, University of Texas, Austin 12, Texas; J. W. Durham, Dept. Paleontology, University of California, Berkeley 4, Calif.; I. R. Hessland, Dept. Geology, University of Stockholm, Stockholm, Sweden; Stuart A. Levinson, Humble Oil & Refg. Co., Box 2180, Houston, Texas; A. K. Miller, Dept. Geology, State University of Iowa, Iowa City, Iowa; M. B. Stephenson, Stanolind Oil and Gas Co., Box 3092, Houston, Texas; Erik Kjellesvig-Waering, Helmerich & Payne, Inc., First National Bank Bldg., Tulsa 3, Okla.; Teiichi Kobayashi, Department of Geology, University of Tokyo, Tokyo, Japan.

THE JOURNAL OF PALEONTOLOGY is published bi-monthly. The numbers issued in January, May, and September are sponsored by The Paleontological Society in cooperation with The Geological Society of America; those issued in March, July, and November are sponsored by The Society of Economic Paleontologists and Mineralogists in cooperation with The American Association of Petroleum Geologists.

The subscription price of the JOURNAL OF PALEONTOLOGY is $10.00 per year prepaid to addresses in the United States.

Single numbers, $2.00 each to nonmembers, $1.50 to members.

Postage is charged extra for all other countries in the Postal Union, 40 cents on annual subscriptions (total $10.40).

THE JOURNAL will furnish reprints at cost. Orders should accompany manuscript.

Communications about the JOURNAL, subscriptions, rates, memberships, change of address, and nonreceipt of preceding numbers should be addressed to Society of Economic Paleontologists and Mineralogists, P. O. Box 979, Tulsa 1, Oklahoma. Claims for nonreceipt of preceding numbers must be sent in within three months of the date of publication in order to be filled gratis. Communications in regard to advertising should be addressed to T. H. Philpott, The Carter Oil Company, Denver, Colorado.

Communications in regard to manuscripts or purely editorial matters should be addressed to Grover E. Murray, School of Geology, Louisiana State University, Baton Rouge 3, Louisiana, or to William R. Evitt, University of Rochester, Rochester 3, N. Y.

Contributors are requested to instruct their photographers to illuminate fossils from the upper left side, the conventional manner. Plates normally should be arranged for publication at the size of 5½ by 7½ inches, exclusive of margins, heading, and title. Printed numerals of standard size and form may be obtained free from either editor. When requesting them state number of plates and the dimensions of each plate.

A statement of style, form and procedure for the JOURNAL, published in Volume 25, no. 5, is available in reprint form on request to either editor.

Entered as second-class matter at the Post Office at Tulsa 1, Oklahoma, under the Act of March 3, 1879. Acceptance for mailing at special rate of postage provided for in paragraph 4, section 538, P. L. and R. authorized April 3, 1935.

Additional entry as second-class matter at the Post Office at Menasha, Wis.

Printed in U.S.A.

GEORGE BANTA PUBLISHING COMPANY, MENASHA, WIS.

JOURNAL OF PALEONTOLOGY

A publication of THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS *and* THE PALEONTOLOGICAL SOCIETY *with the generous support and cooperation of* THE AMERICAN ASSOCIATION OF PETROLEUM GEOLOGISTS *and* THE GEOLOGICAL SOCIETY OF AMERICA

VOLUME 28 JANUARY, 1954 NUMBER 1

FAUNAS AND AGE OF THE AMSDEN FORMATION IN WYOMING

C. A. BURK

University of Wyoming, Laramie, Wyoming

ABSTRACT—A review of the fossils identified from the Amsden formation by previous workers indicates a Pennsylvanian rather than a Mississippian age for the Amsden in Wyoming. Six new faunas from the formation are believed to be Pennsylvanian in age, and include the following identifiable genera and species: *Dictyoclostus portlockianus, Linoproductus prattenianus, Cancrinella boonensis, Marginifera muricatina, Spirifer opimus, Composita subtilita* var. *subtilita, C. subtilita* var. *trinuclea, C. subtilita* var. *ovata, Wellerella osagensis, Allorisma terminale, Lingulodiscina, Marginifera, Spirifer, Composita, Naticopsis, Orthotetes?, Cleiothyridina?*, and an unidentifiable tetracoral and goniatite. One new species is proposed, *Eumetria sulcata.*

INTRODUCTION

THE Amsden formation of Wyoming, Montana, and Utah has been frequently studied and discussed since it was named and defined by N. H. Darton (1904, pp. 396–397), yet there has been no general agreement concerning its age and stratigraphic limits. Most of the published stratigraphic sections have recently been remeasured by C. A. Biggs, and additional sections measured, in an attempt to delimit and correlate the lithologic units of the Amsden. The results of this study are reported in an unpublished Master's thesis on file at the University of Wyoming. A sizeable collection of fossils was obtained by Biggs from several localities and units in the formation. This collection forms the basis for this paper.

I should like to express my sincere appreciation for the time given to me by Mr. Biggs in explaining the results of his work on the Amsden formation in Wyoming and the many stratigraphic problems involved. He also prepared all of the specimens for study.

This paper would not have been possible without the patience and guidance of Dr. Alan B. Shaw of the Department of Geology, University of Wyoming, to whom I am most sincerely indebted. I am grateful to Dr. H. D. Thomas of the Department of Geology, University of Wyoming, and the State Geologist of Wyoming, who read and criticized the manuscript; in addition, the Wyoming Geologic Survey supplied the film for the photographs included in this paper.

LITHOLOGY OF THE AMSDEN FORMATION

The Amsden formation of northwestern Wyoming consists of 150 to 350 feet of a somewhat variable succession of sandstones, red shales, limestones, dolomites, and cherts, with a basal member (the Darwin sandstone) of 50 to 150 feet of massive, generally tan, sandstones. The Darwin sandstone unconformably overlies the Mississippian Madison limestone, and the Amsden forma-

tion is overlain conformably by the Pennsylvanian Tensleep sandstone.

REVIEW OF THE LITERATURE

Because of the controversy over the age of the Amsden formation, it is first necessary to review all the literature in which Amsden faunas are mentioned. The history of the nomenclature and the present stratigraphic limits of the Amsden are shown in Figure 1. All generic assignments included in the following discussions are as they appeared in the original faunal lists, and are not necessarily in accord with modern taxonomy.

Darton (1906, pp. 33–34), while working in the central Bighorn Mountains west of Sheridan, Wyoming, collected a coral from the lower Amsden limestone which was identified by Girty as *Menophyllum excavatum*. Girty also identified ten other species collected by Darton from the upper cherty beds near the North Fork of Crazy Woman Creek in this same area: *Productus nebrascensis*, *Edmondia nebrascensis*, *Archaeocidaris* sp., *Murchisonia* aff. *M. lasallensis*, *Orthotetina* n. sp., *Aviculopecten occidentalis?*, *Pleurophorus* aff. *P. subcostatus*, *Euomphalus catilloides?*, *Pleurotomaria scitula?*, and *Bellerophon?* sp. Darton believed that this evidence indicated that the lower part of the formation is Mississippian in age and that the upper part is Pennsylvanian.

Blackwelder (1913, pp. 175–176) collected fossils from two zones near the middle of the Amsden along the crest of the Gros Ventre Mountains in northwestern Wyoming. These faunas were identified by Girty as follows: Upper (Brachiopod) Zone—*Echinocrinus* sp., crinoidal plates, *Batostomella* sp., *Rhombopora lepidodendroides?*, *Stenopora* sp., *Lingula umbonata?*, *L. carbonaria*, *Lingulodiscina* sp., *Derbyia robusta*, *Schizophoria* aff. *S. resupinoides*, *Chonetes geinitzianus*, *C. granulifer*, *Productus cora*, *P. semireticulatus*, *P. nebrascensis*, *Spirifer rockymontanus*, *Composita subtilita*, *Conocardium* sp., and a fish plate; Lower (Mollusk) Zone—large crinoidal stems, *Spirifer rockymontanus?*, *Squamularia perplexa?*, *Composita subtilita?*, *Myalina* sp., *Cypri-*

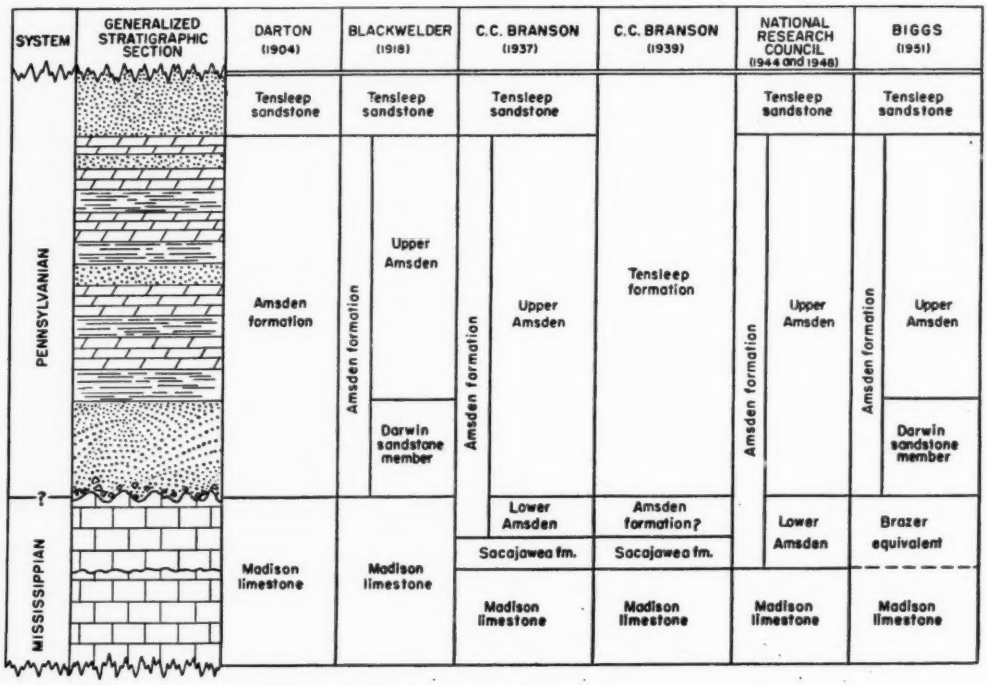


FIG. 1—History of the nomenclature of the Amsden and associated formations in northwestern Wyoming (modified after Biggs, 1951).

cardinia sp., *Pleurophorus* two sp., *Bucanopsis?* sp., *Euphemus?* sp., *Pleurotomaria* sp., *Naticopsis* sp., and *Euomphalus* sp.

Girty believed that the fauna of the upper horizon was definitely of Pennsylvanian age, but that the fauna of the lower horizon might be of Mississippian age. Of this Blackwelder (1913, p. 177) says, "Both faunules occur in a single formation of unified and distinctive character, separated from the known Mississippian rocks by a distinct unconformity. Therefore, unless there is strong evidence to the contrary, it seems probable that both faunules belong to the same period."

E. B. Branson and Greger (1918, p. 312) collected from what they believed to be the Amsden formation at Bull Lake Canyon and Cherry Creek in the Little Popo Agie region of the Wind River Mountains west of Lander, Wyoming. Biggs revisited these localities and demonstrated that their collection from Bull Lake Canyon was taken from the Mississippian Madison limestone, but that it is possible that part of their collection from Cherry Creek was taken from the lower Amsden. This cannot be established, however, since the beds are very poorly exposed and Biggs points out that the fossils could apparently be obtained only from slope wash. In view of this discovery, the fossils they obtained from Bull Lake Canyon cannot be used as a basis for dating the Amsden.

Because the Branson and Greger collections were the only ones described and figured, they became a standard reference for later geologists, and on this basis, the apparent Mississippian age of the Amsden was generally accepted by many Rocky Mountain geologists.

Lee (1927, p. 72) listed nine species identified by Girty, which were taken from the top limestone of the Amsden in the Wind River Range near Lander, Wyoming. Lee states that the Amsden of this area seems to correspond to beds in the Gros Ventre Range which Blackwelder (1913, pp. 175–176) found to contain many Pennsylvanian fossils. Lee's collection contained the following species: *Derbyia crassa?*, *Chonetes granulifer* var., *Productus cora*, *P. hermosanus*, *Pustula semipunctata*, *Marginifera splendens*, *Spirifer rockymontanus*, *Squamularia perplexa*, and *Composita subtilita*.

Morey (1935, pp. 475–482) described 17 species of ostracodes from the same localities in which Branson and Greger (1918) made their collections. All the specimens were collected from float which was estimated to have originated from somewhere near the middle of the Amsden formation. His collection included the ubiquitous *Paraparchites nicklesi* and 16 new species. Morey states that the age of this fauna is Mississippian, and probably Ste. Genevieve; but since his collection was taken from slope wash in Branson's and Greger's (1918) area, which was shown by Biggs to include the Mississippian Madison limestone, his conclusions cannot be regarded as bearing on the age of the Amsden formation.

C. C. Branson (1939, pp. 1201, 1213, 1217) reviewed and examined some of the faunas of earlier workers and added his own identifications to those already listed. Branson identified the following species from the fauna first listed by Darton (1906, pp. 33–34): *Derbyia* sp., *Orthotetina* sp., *Juresania nebrascensis*, *Edmondia* sp., *Deltopecten* sp., *Pleurophorus* sp., *Euomphalus* sp., *Pleurotomaria* sp., *Bellerophon* sp., and *Ameura major*. Branson stated that the age of this fauna is certainly Pennsylvanian. He listed the following identifications from the fauna first reported by Lee (1927, p. 72): *Linoproductus prattenianus*, *Dictyoclostus hermosanus*, *Echinoconchus semipunctatus?*, *Chonetes* sp., *Composita subtilita*, and *Cleiothyridina?* sp. Branson believed that these species undoubtedly represent a Tensleep (Pennsylvanian) fauna and were probably not collected from the Amsden. Branson made the following identifications from the fauna first listed by Blackwelder (1913, pp. 175–176): Upper Fauna—*Lingula* sp., *Lingulodiscina* sp., *Derbyia crassa*, *Juresania nebrascensis?*, *Dictyoclostus hermosanus*, *Linoproductus prattenianus*, *Chonetes granulifer*, *Composita subtilita*, *Spirifer rockymontanus*, *Pleurophorus* sp., *Conocardium* sp., and crinoid, echinoid, and bryozoan remains; Lower Fauna—*Composita subtilita*, *Squamularia perplexa*, and *Spirifer rockymontanus*. Branson indicated he believed that these faunas are also characteristic of the Pennsylvanian Tensleep sandstone rather than the Amsden formation.

Love (1939, p. 28) collected fossils from a unit 66 feet above the base of the Amsden along the southern margin of the Absaroka Range, and identified the following forms: *Composita trinuclea, Spirifer pellaensis, Spiriferina?* sp., *Bellerophon?* sp., *Chonetes* sp., and four species of productids, a small horn coral, a loosely-coiled gastropod, and a large, high-spired gastropod. From a unit 200 feet above the base of the Amsden (10 feet below the top of the Amsden) Love collected several flat-spired gastropods and two silicified fusulinids identified as *Fusulinella* sp. The presence of these fusulinids would seem to demonstrate an Oklan age for at least the upper part of the Amsden.

MISSISSIPPIAN-PENNSYLVANIAN BOUNDARY

The Pennsylvanian Subcommittee of the National Research Council (Moore et al., 1944, p. 663) recognizes the Mississippian-Pennsylvanian boundary as follows: "The base of the Pennsylvanian is generally defined by (1) occurrence of an obviously significant structural discordance, (2) an important sedimentary hiatus, (3) a pronounced lithologic change, and (4) readily determined paleontologic evidence." The Mississippian Subcommittee reached the same conclusions regarding the upper boundary of the Mississippian, and added that "the magnitude, importance, and extent of this unconformity is one of the principal reasons for the recognition of the Mississippian and Pennsylvanian as independent systems by most American geologists." (J. M. Weller et al., 1948, p. 106.) All of these physical criteria normally characterizing the Mississippian-Pennsylvanian boundary were shown by Biggs to be present at the base of the Amsden formation.

Weller et al. (1948, p. 140) state that "Blackstone, Love, and Thomas recognize a widespread unconformity at the base of the Darwin sandstone, which they consider to be the lowest member of the Amsden, and they refer the entire formation . . . to the Pennsylvanian." Biggs concludes that "on the basis of regional relationships and stratigraphic position . . . the Amsden is entirely Pennsylvanian in age. The lowest part of the Amsden is probably Atokan or older, while the upper part is Desmoinesian or older."

AGE AND FAUNAL CONSIDERATIONS

No fossils have yet been collected from the Darwin sandstone member of the Amsden, and fossils are generally scarce throughout the formation. Those forms which have been reported in the literature have appeared mainly in faunal lists, and many of these were given only generic assignments.

There is no previously described fauna of known age which is comparable to the assemblage of fossils which has gradually been taken from the Amsden. In order to establish the age of the Amsden, it is necessary therefore, to examine the known ranges of all those forms which have been collected from beds above the Darwin sandstone. All of the Madison fossils, mistakenly assigned to the Amsden, are omitted from consideration, as well as those forms which were identified with hesitation. New species taken from the Amsden are also excluded from this tabulation.

The accompanying series of diagrams (Figs. 2–5) shows graphically the results of these range considerations. Those forms which were identified only to genus are separated in Figures 2–5 from those forms which were specifically identified. This is done of necessity because the ranges of the identified genera are in most cases greater than the ranges of the identified species.

Figure 2 shows the distribution by ranges of genera and species identified in previously published faunal lists. The majority of those forms identified specifically are known only from strata of Pennsylvanian age, and all of those forms which are exclusively Pennsylvanian are identified to species. The majority of forms having a range which includes both the Mississippian and Pennsylvanian are identified only to genus. No genus or species is exclusively Mississippian or older. Thus, it is apparent that none of the previously identified faunas have a range which conflicts with a Pennsylvanian age for the Amsden.

Figure 3 shows the distribution by ranges of the genera and species of the faunas described in this paper. The similarity in distribution of ranges with the previously described faunas (Fig. 2) is apparent, and in both instances the ratio between generic and specific identifications is nearly identi-

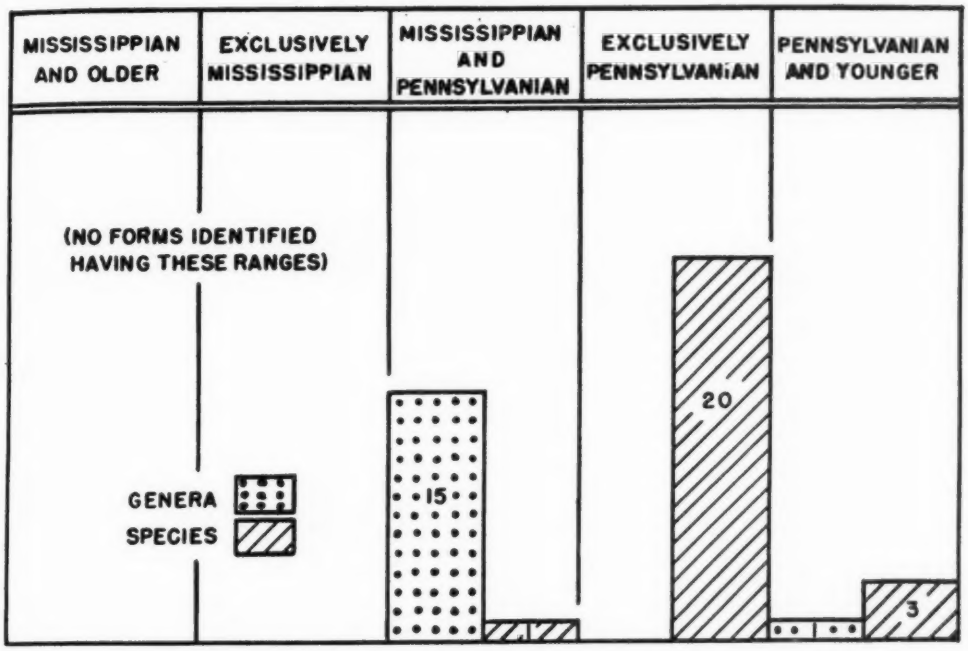


FIG. 2—Diagram showing distribution of Amsden fossils previously identified in published faunal lists.

cal. Figure 4 combines Figures 2 and 3 and presents the distribution of all forms identified from the Amsden, omitting all duplications.

Figure 5 shows the distribution of the total number of individual specimens in the present collection, according to the ranges of the identified genera or species. This shows that the large majority of the specimens are of species known only from rocks of Pennsylvanian age and younger.

Several conclusions are apparent from this series of figures. In each instance the greatest number of species are Pennsylvanian in age. There are no identifications which would conflict with a Pennsylvanian age for the Amsden, and there is none which supports an exclusively Mississippian age. If all the forms now generically identified, having a range including both the Mississippian and Pennsylvanian, were found to have been taken from the lower part of the Amsden it might suggest a late Mississippian age for this part of the formation, but an examination of all the faunal lists and the present collection shows that there are as many exclusively Pennsylvanian species known from just above the Darwin sandstone as there are genera and species which have a range including both the Mississippian and Pennsylvanian.

Further collection and study of Amsden fossils might make it possible to determine the Pennsylvanian series represented by Amsden deposits, but the present collection is too inadequate to form such conclusions. However, the faunal evidence pointed out in this paper makes it necessary to abandon the Mississippian age previously accepted for the Amsden, and confirms its Pennsylvanian age, in accord with the physical and stratigraphic relationships most recently discussed by Biggs.

LOCALITIES AND FAUNAS

The faunal localities are identified here according to the system used in the paleontologic collections at the University of Wyoming. The first two digits of the numerator show the township; the second two or three digits indicate the range. The denominator indicates the section and is followed by a letter to discriminate collections taken from the same section. The locations of the col-

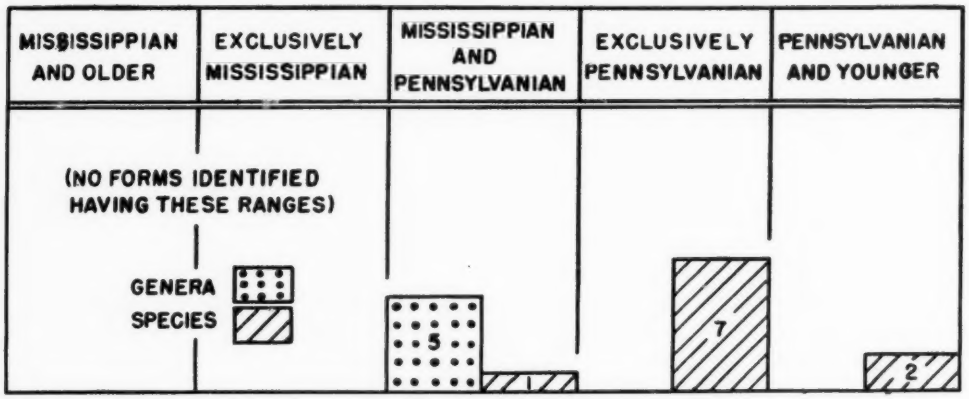


FIG. 3—Distribution by ranges of the fossils examined in the present faunas.

lections are shown on the map in Figure 6.

$\frac{2997}{6A}$···NW¼, Sec. 6, T. 29 N., R. 97 W., Beaver Creek, Fremont Co., Wyoming: 45 feet above the contact with the Madison limestone, in a pisolitic hematite bed. The collection contained three specimens, one each of *Spirifer opimus*, *Composita* sp., and an unidentifiable tetracoral.

$\frac{3099}{9A}$···Center, Sec. 9, T. 30 N., R. 99 W., South Pass, Fremont Co., Wyoming: 55 feet above the contact with the Madison limestone, in a buff to tan, fine-grained shale. The collection contained 51 specimens of the following species: *Linoproductus prattenianus* (3), *Cancrinella boonensis* (2), *Marginifera muricatina* (23), *Spirifer opimus* (16), *Cleiothyridina?* sp. (3), and *Allorisma terminale?* (4).

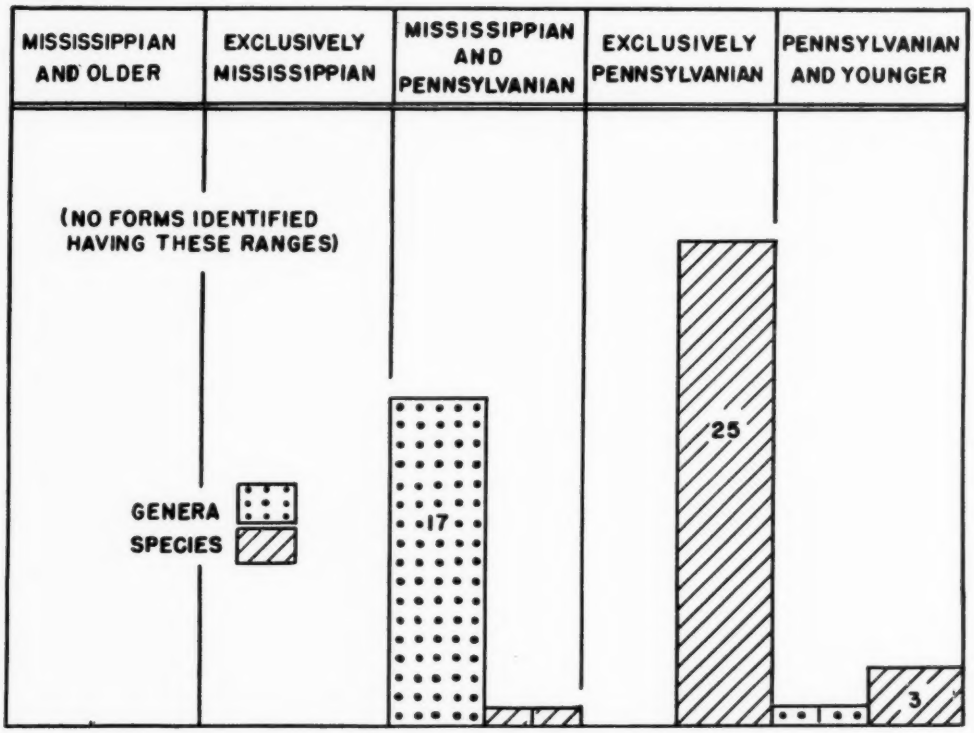


FIG. 4—Diagram showing distribution by ranges of all the forms identified to genus or to species which were taken from the Amsden formation in Wyoming.

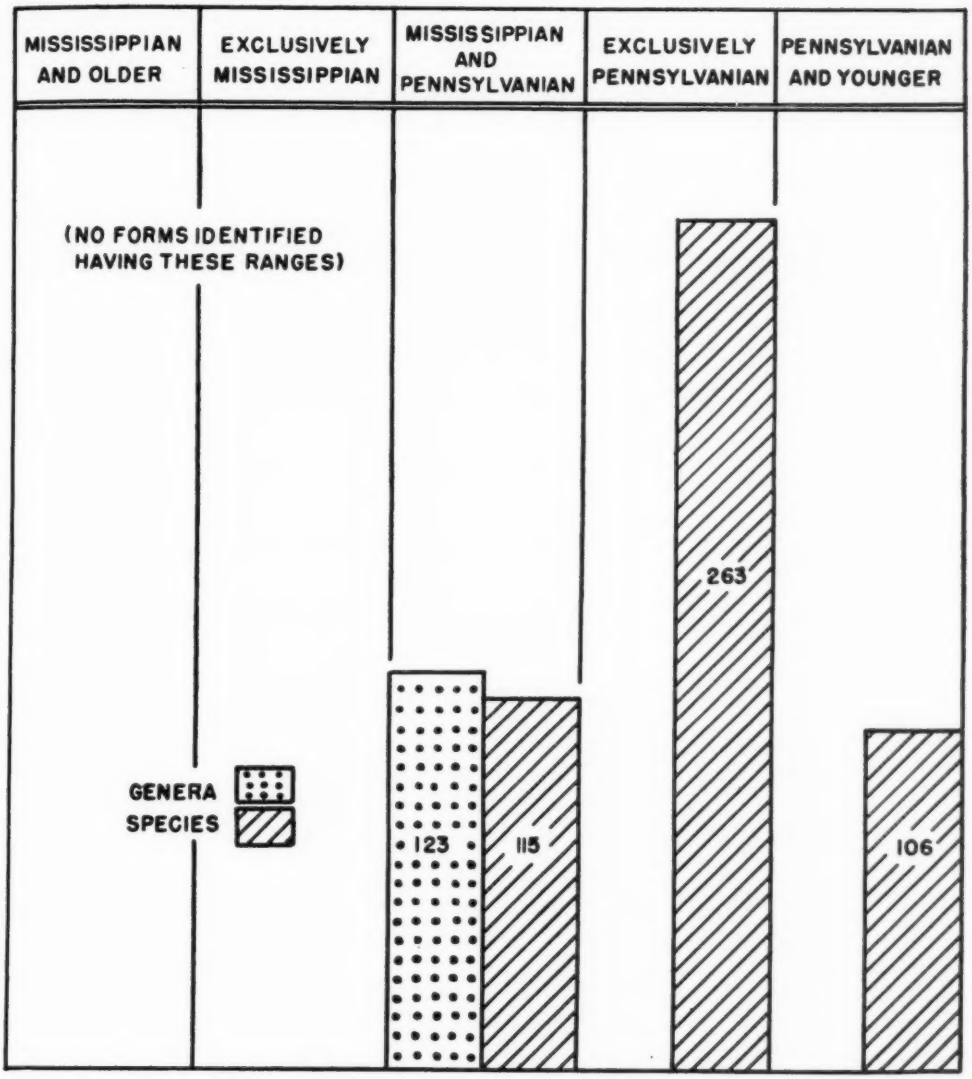


FIG. 5—Distribution by ranges of the number of identifiable specimens in the present faunas.

$\frac{3099}{9B}$···Center, Sec. 9, T. 30 N., R. 99 W., South Pass, Fremont Co., Wyoming: 50 feet above the contact with the Madison limestone, in a medium-grained, ferruginous sandstone. The collection contained 15 specimens of the following species: *Wellerella osagensis* (2), *Lingulodiscina* sp. (4), *Dictyoclostus portlockianus* (1), and *Spirifer opimus* (8).

$\frac{3199}{19A}$···NW¼, Sec. 19, T. 31 N., R. 99 W., Cherry Creek, Fremont Co., Wyoming: 60 to 90 feet above the contact with the Madison limestone, in float. The collection contained 483 silicified specimens of the following species: *Marginifera* sp. (1), *Spirifer opimus* (95), *Composita subtilita* var. *subtilita* (97), *C. subtilita* var. *trinuclea* (109), *C. subtilita* var. *ovata* (48), *Composita* sp. (93), *Wellerella osagensis* (31), *Eumetria sulcata* (7), *Marginifera* sp. (1), and an unidentified goniatite.

$\frac{43106}{19A}$···SW¼, Sec. 19, T. 43 N., R. 106 W., Horse Creek, Fremont Co., Wyoming: 90 feet above the contact with the Madison limestone, in a yellow to red shale below a resistant purple limestone unit. The collection contained 16 specimens of *Composita subtilita* var. *ovata*, and one of *Cleiothyridina* sp.

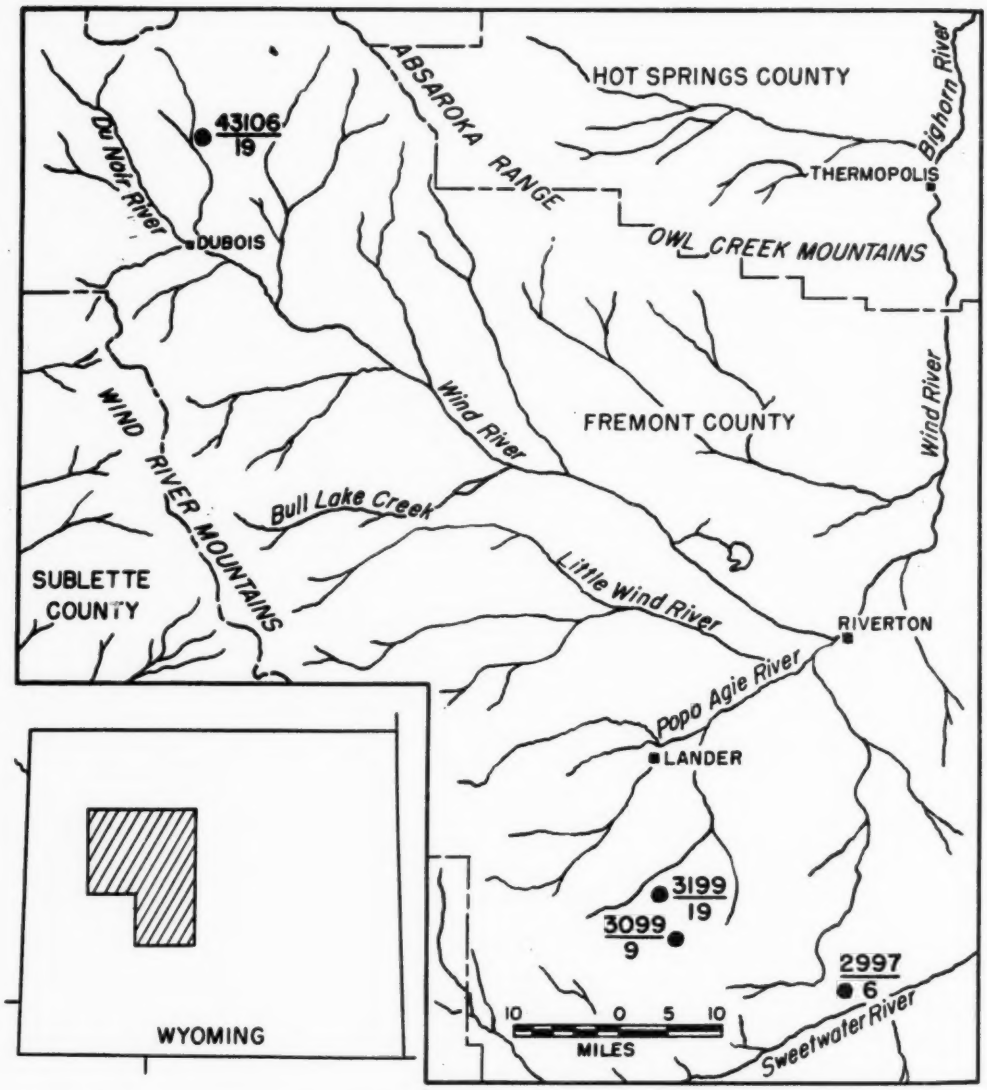


FIG. 6—Index map showing locations of faunal collections examined in this paper.

$\frac{43106}{19B}$···SW¼, Sec. 19, T. 43 N., R. 106 W., Horse Creek, Fremont Co., Wyoming: 94 feet above the contact with the Madison limestone, in a resistant purple limestone unit. The collection contained 59 specimens, 48 of which were silicified. The following species were identified: *Orthotetes?* sp. (1), *Dictyoclostus portlockianus* (8), *Linoproductus prattenianus* (2), *Spirifer* sp. (5), *Composita subtilita* var. *subtilita* (5), *C. subtilita* var. *trinuclea* (6), *C. subtilita* var. *ovata* (3), *Composita* sp. (10), *Cleiothyridina* sp. (11), *Wellerella osagensis* (4), and *Allorisma terminale* (4).

SYSTEMATIC PALEONTOLOGY

Phylum BRACHIOPODA
Genus LINGULODISCINA Whitfield, 1890
LINGULODISCINA sp.
Plate 1, figures 13, 14

Four dorsal valves of this genus were obtained from the collection. They are most similar to shells of *Lingulodiscina pleurites* (Meek), 1875, but are more lenticular in their mature outline and are considerably

less rounded on the posterior margin. The specimens represent an ontogenetic sequence: the smallest, with a diameter of 5.0 mm., is nearly circular in outline with a nearly centrally situated conical apex. The most mature specimen measures 23 mm. from the anterior to the posterior margin, and 22 mm. at the greatest width, which is 7 mm. from the anterior margin; the valve is highly depressed-conical with its apex projecting posteriorly, parallel to the plane of the valves and overreaching the posterior line of commissure. The valves are concentrically ornamented with elliptical growth lines, which are farthest apart along the anterior slope of the valve and closest along the posterior slope.

These specimens may represent an undescribed species, but insufficient material is at hand to justify erecting a new name.

Locality.— $\frac{3099}{9B}$.

Figured specimens.—U. Wyo. IT-184, IT-185.

Other specimens.—U. Wyo. IT-186.

Genus ORTHOTETES Fischer de Waldheim, 1837

ORTHOTETES? sp.
Plate 1, figure 1

A single, large, incomplete and poorly preserved specimen is here referred to *Orthotetes* with some doubt. Neither the outline nor the shape of the valve has been preserved. Only part of the surface ornamentation is apparent, and it is on this basis alone that the specimen is referred to this genus. The ornamentation of the Orthotetinae is generally not of generic importance, but the ribbing of this specimen does not resemble that of any of the other large genera as much as it does *Orthotetes*.

The valve is marked by prominent radial costae, separated by single, smaller ribs. Concentric ornamentation is present as indefinite, irregular growth lines. The valve is at least 30 mm. long at the median line, and 30 mm. at the greatest width.

Locality.— $\frac{43106}{19B}$.

Specimen.—U. Wyo. IT-187.

Genus DICTYOCLOSTUS Muir-Wood, 1930

DICTYOCLOSTUS PORTLOCKIANUS (Norwood and Pratten)
Plate 1, figures 29, 30

Productus portlockianus NORWOOD & PRATTEN, 1854, Acad. Nat. Sci. Philadelphia Jour., vol. 3, p. 15, pl. 1, figs. 9a–c.
Productus inflatus var. *coloradoensis* GIRTY, 1915, U. S. Geol. Survey Bull. 544, pp. 64–65, pl. 8, figs. 1–2.
Dictyoclostus portlockianus DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2nd ser., pp. 215–217, pl. 33, figs. 1–3.

The shells are medium sized, with the length approximately equal to the width. The ventral valve is strongly convex and geniculate. The ventral beak is incurved over the hinge line, and the cardinal extremities are moderately auriculate. A ventral sulcus is irregularly developed, and where present it is shallow, narrow, and originates in the middle of the umbo. Spines are irregularly scattered along the costae of the ventral valve. The dorsal valve is gently concave over the visceral cavity and sharply geniculate anteriorly. The umbo is strongly semireticulate.

Although many specimens are fragmentary and exfoliated, they show as a group the typical features of the species. Shells most similar to *Dictyoclostus portlockianus* (Norwood and Pratten) are those of *D. inflatus* (McChesney), 1860 and *D. burlingtonensis* (Hall), 1858 which have a sharp ventral sulcus originating close to the beak, a strongly inflated umbo, and an arc of curvature of short radius from the beak to the tip of the trail.

Localities.— $\frac{3099}{9B}$, $\frac{43106}{19B}$.

Figured specimens.—U. Wyo. IT-188, IT-189.

Other specimens.—U. Wyo. IT-190, IT-191.

Genus LINOPRODUCTUS Chao, 1927

LINOPRODUCTUS PRATTENIANUS (Norwood)
Plate 1, figures 36, 37

Productus prattenianus NORWOOD in Norwood & Pratten, 1854, Acad. Nat. Sci. Philadelphia Jour., vol. 3, p. 17, pl. 1, figs. 10a–d.
Productus prattenianus MEEK, 1872, U. S. Geol. Survey Nebraska, Final Rept.; p. 163, pl. 2, fig. 5; pl. 5, fig. 13; pl. 8, fig. 10.

Linoproductus prattenianus DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2nd ser., pp. 241–244, pl. 26, figs. 1–5, 9.

The shell is medium sized, with the hinge line equal to the greatest width of the shell. The ventral valve is subhemispherical and evenly convex from the beak to the trail. The ventral beak is small, pointed, and closely incurved over the hinge line. The surface of the ventral valve is finely costate, the costae increasing by implantation, and numbering from two to three costae per millimeter on the trail. The cardinal extremities are moderately wrinkled. Spines are small and the spine bases, scattered across the surface of the ventral valve, are inconspicuous. The dorsal valve is moderately concave and moderately geniculate.

All of the specimens in the collection are fragmentary or distorted, but as a group they clearly show the characters typical of the species. *Linoproductus prattenianus* is distinct from *L. ovatus* (Hall), 1858, because it contains shells having subequal dimensions, moderate concavity and geniculation of the dorsal valve, and distinct cardinal extremities arising sharply from the convex umbo.

Localities.— $\frac{3099}{9A}$, $\frac{43106}{19B}$.

Figured specimens.—U. Wyo. IT-192, IT-193.

Other specimens.—U. Wyo. IT-194.

Genus CANCRINELLA Fredericks, 1928
CANCRINELLA BOONENSIS (Swallow)
Plate 1, figure 35

Productus boonensis SWALLOW, 1858, Acad. Sci. St. Louis Trans., vol. 1, p. 217.

Productus pertenuis MEEK, 1872 (part), U. S. Geol. Survey Nebraska, Final Rept., p. 164, pl. 1, figs. 14a–c (not pl. 8, figs, 9a–d).

Cancrinella boonensis DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2nd ser., pp. 258–260, pl. 32, figs. 1–5.

The shells are very small, the visceral area nearly circular, having a diameter of about 5 mm. The dorsal valve is flat to slightly concave and is not sharply geniculate. The ventral valve is only moderately convex and slopes gently toward the margins of the valve. The cardinal extremities are concentrically wrinkled, with the broad rugae extending over the umbonal area, but becoming indistinct toward the trail. This concentric ornamentation almost completely obscures the radial costae on the umbo. The costae are broad and flat, and are especially prominent near the trail. The spines and spine bases are most abundant on the lateral margins and cardinal extremities of the ventral valve.

The collection contains a single fragmentary ventral valve and an impression of a ventral valve. The ornamentation is clearly shown on this impression and is typical of the species, but the outline of the valve is not well preserved on either specimen. Both are about 5 mm. in diameter across the nearly circular visceral region.

Locality.— $\frac{3099}{9A}$.

Figured specimens.—U. Wyo. IT-195.

Other specimens.—U. Wyo. IT-196.

Genus MARGINIFERA Waagen, 1884
MARGINIFERA MURICATINA
Dunbar and Condra
Plate 1, figures 26–28

Productus muricatus NORWOOD & PRATTEN, 1854, not Phillips, 1836, Acad. Nat. Sci. Philadelphia Jour., vol. 3, 2nd ser., pp. 14–15, pl. 1, figs. 8a–e.

Marginifera muricata GIRTY, 1915, not Phillips, 1836, U. S. Geol. Survey Bull. 544, pp. 78–79, pl. 10, figs. 3–4a.

Marginifera muricatina DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2nd ser., pp. 222–224, pl. 35, figs. 1–10.

Marginifera? muricatina COOPER in Shimer & Shrock, 1944, Index Fossils of North America, p. 351, pl. 137, figs. 24–26, John Wiley, New York.

The shells are small; a typical specimen is 1.8 cm. wide and 1.5 cm. long. The ventral valve is moderately and evenly convex from the beak to the trail. The hinge line is equal to or slightly less than the greatest width of the shell. The cardinal extremities are broadly angular or rounded. The dorsal valve is slightly to deeply concave. The trail is relatively short. The ventral sulcus is obsolete or entirely lacking, and the ventral valve is ornamented with coarse, irregular costae bearing numerous, scattered spine bases. Concentric rugae are more or less prominent at the beak and cardinal extremities but are absent on the trail. The

marginal flange of the interior of the dorsal valve is obsolete medially.

This species is recognizable by its coarse ribbing, incomplete marginal flange, and by the obsolescence or absence of the ventral sulcus. The collection contained 23 fragmentary specimens of this species.

Locality.— $\frac{3099}{9A}$.

Figured specimens.—U. Wyo. IT-197, IT-198.

Other specimens.—U. Wyo. IT-199.

MARGINIFERA sp.

The collection contained a single specimen which is silicified and fragmentary and only a part of the umbo, hinge line, and beak are present. It is not *M. muricatina*, as shown by the presence of a ventral sulcus on the umbo and a lack of reticulation at the beak. The shell was probably somewhat larger than the specimens of *M. muricatina* in the collection, and the ribbing is more irregular and discontinuous.

Locality.— $\frac{3199}{19A}$.

Specimen.—U. Wyo. IT-200.

Genus SPIRIFER Sowerby, 1818

SPIRIFER OPIMUS Hall

Plate 1, figures 16–22

Spirifer opimus HALL in Hall & Whitney, 1858, Report on the geological survey of Iowa (1855–1857), vol. 1, pp. 711–712, pl. 27, figs. 1a–b.

Spirifer opimus DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2nd ser., pp. 320–322, pl. 43, figs. 10a–11b.

The shell is medium sized, moderately alate, and approximately as wide as long. The interareas are prominent, the dorsal being about one-fourth the height of the ventral, and the ventral interarea is marked by prominent vertical striations. There are initially three costae on the dorsal fold, but the central rib splits in the umbonal area to form two closely associated ribs which remain more prominent than the bordering costae. The lateral slopes show 8–10 ribs, most commonly eight. The ventral sulcus has three costae throughout most of its length, and there are normally eight costae on each lateral slope. The fold and sulcus are very pronounced, giving the shell a robust lateral profile.

Shells of this species can be distinguished from other spiriferaceans by their characteristic 8–10 lateral costae, subovate outline, prominent fold and sulcus, and the splitting of the central plication in the umbonal area.

Spirifer opimus is most similar to *S. leidyi* Norwood and Pratten, 1855, a Mississippian species, but can be recognized by the splitting of the lateral costae of the fold. Apparently these two species and *S. rockymontanus* Marcou, 1858, are very closely related.

The collection contained 120 specimens which could be referred to *S. opimus*, most of which are silicified and distorted, but together they show all of the features typical of the species.

Localities.— $\frac{2997}{6A}$, $\frac{3099}{9A}$, $\frac{3099}{9B}$, $\frac{3199}{19A}$.

Figured specimens.—U. Wyo. IT-201, IT-205.

Other specimens.—U. Wyo. IT-206, IT-209.

SPIRIFER sp.

Three fragmentary ventral valves and two fragmentary dorsals may represent an undescribed species but the collection is too incomplete to verify this possibility. They do not show the typical bifurcation of the lateral costae on the fold of *Spirifer opimus*.

The shells are alate, of small size, and moderately biconvex. The surfaces of the valves are marked by twelve angular costae, with two in the ventral sulcus and two on the high, narrow dorsal fold. Both valves are most convex in the umbonal region and are nearly plane anteriorly.

Locality.— $\frac{43106}{19B}$.

Specimens.—U. Wyo. IT-210.

Genus COMPOSITA Brown, 1845

Genotype.—*Spirifer ambiguus* Sowerby, 1821.

The shell is biconvex, subpentagonal or subovate in outline, with a uniplicate to parasulcate line of commissure. The hinge line is short and interareas are lacking.

The ventral beak is incurved over the obtuse dorsal beak. The delthyrium is nearly closed dorsally in adult forms, leaving an oval foramen at the tip of the beak. A dorsal fold and ventral sulcus are most prominent on the anterior part of the shell. The shell is smooth, except for the irregularly spaced concentric growth lines. The shell matter is impunctate and fibrous. The hinge teeth are supported by flange-like dental lamellae that are usually fused to the sides of the valve. Crura arise from the anterior margin of the hinge plate, and bear inflated, laterally directed spiralia.

Shells of this genus can be recognized among other rostrospiraceans by the absence of a dorsal median septum, and a hinge plate which is sub-quadrate in shape.

Separation of species.—The genus *Composita* includes common, long-range forms which are of little stratigraphic significance. The species are gradational and difficult to separate, as the morphology of the shell is simple and shows little distinctive variation. The discrimination of these species has been a continual problem to geologists wherever specimens of this genus have been encountered. This problem was discussed by Weller (1914, pp. 485–486) and by Dunbar and Condra (1932, pp. 363–369).

Three general shapes were recognized in the present collections which are comparable to the general forms commonly assigned to the species *Composita subtilita* (Hall), 1853, *C. trinuclea* (Hall), 1858, and *C. ovata* Mather, 1915. The features used to distinguish these groups are the general outline of the shell, which varies from ovate to sub-pentagonal, and the nature of the line of commissure, which progresses from uniplicate to strongly parasulcate. These features are discussed further under the diagnosis of the varieties, but it should be pointed out that although they are very prominent for typical forms, there is a gradation from the typical specimen of one group to the typical specimen of another group and many transitional specimens are difficult to assign to one particular form.

Inasmuch as it is impossible to separate clear-cut species within this genus, the most useful procedure seems to be to recognize varieties of a single species. The species *Composita trinuclea* and *C. ovata* will here be considered as varieties of *C. subtilita*. Typical specimens of these varieties are contrasted in figures 2–10 of Plate 1, and their most distinguishing characters are given in Table 1.

TABLE 1—GENERAL FEATURES OF THE VARIETIES OF *COMPOSITA SUBTILITA* (Hall), 1853

Variety	Anterior Line of Commissure	Outline of Shell
ovata	Uniplicate	Ovate
subtilita	Uniplicate	Sub-pentagonal
trinuclea	Parasulcate	Sub-pentagonal

COMPOSITA SUBTILITA var. SUBTILITA (Hall)
Plate 1, figures 5–7, 12

Terebratula subtilita HALL in Stansbury, 1853, Exploration and Survey of the Valley of the Great Salt Lake of Utah: House Exec. Document, no. 3, p. 409, pl. 4, figs. 1a–b, 2a–c.
Composita subtilita DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2nd ser., pp. 363–366, pl. 43, figs. 7–13.
Composita subtilita COOPER in Shimer & Shrock, 1944, Index Fossils of North America, p. 335, pl. 128, figs. 9–12, John Wiley, New York.

The shells are sub-pentagonal in outline and moderately gibbous. The ventral beak is highly incurved but not so much as to conceal the delthyrium. There is a single dorsal fold and ventral sulcus which are most prominent at the anterior of the shell. The anterior line of commissure is strongly uniplicate to gently parasulcate. Both valves may be marked by more or less prominent lamellose growth lines, especially along the anterior margin (Plate 1, figure 12).

The collections contained 102 silicified specimens of this variety.

Localities.— $\frac{3199}{19A}$, $\frac{43106}{19B}$.

Figured specimens.—U. Wyo. IT-211, IT-212.

Other specimens.—U. Wyo. IT-213, IT-214.

COMPOSITA SUBTILITA var. OVATA Mather
Plate 1, figures 2–4, 11

Composita ovata MATHER, Denison Univ. Sci. Lab. Bull., vol. 18, p. 202, pl. 14, figs. 6–6a.

Composita ovata DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2d ser., pp. 371–374, pl. 43, figs. 14–16.

The shell is medium sized, biconvex but not sharply arched, and flattened rather than gibbous. The shell is characteristically ovate in outline. The ventral beak is highly incurved, almost concealing the delthyrium. There is a single, slight dorsal fold and ventral sulcus. The fold may be obsolete or absent. The sulcus is narrow and begins near the posterior edge of the shell, extending to the anterior margin of the ventral valve with only a slight increase in prominence. The line of commissure is gently uniplicate. The shell is rarely marked by prominent growth lines.

The collections contained 67 specimens of this variety, most of which are silicified.

Localities.— $\frac{3199}{19A}$, $\frac{43106}{19A}$, $\frac{43106}{19B}$.

Figured specimens.—U. Wyo. IT-215-IT-217.

Other specimens.—U. Wyo. IT-218-IT-220.

COMPOSITA SUBTILITA var. TRINUCLEA (Hall)
Plate 1, figures 8–10

Terebratula trinuclea HALL, 1858, Albany Inst. Trans., vol. 14, p. 7.
Composita trinuclea WELLER, 1914, Illinois Geol. Survey Mon. 1, pp. 486–488, pl. 81, figs. 16–45.
Composita trilobata DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2d ser., pp. 372–373, pl. 43, figs. 25–31.
Composita trinuclea COOPER in Shimer & Shrock, 1944, Index Fossils of North America, p. 335, pl. 128, figs. 16–20, John Wiley, New York.

Shells are medium sized, sub-pentagonal in outline, biconvex, and gibbous. The ventral beak is highly incurved, but not so much as to conceal the delthyrium. The anterior line of commissure is prominently parasulcate. The median ventral sulcus is apparent even on the posterior half of the valve, but the lateral sulci are less prominent. Both valves are marked in well-preserved specimens by lamellose growth lines, especially along the margins of the shell.

Dunbar and Condra (1932, pp. 372–373) described a group of shells from the Pennsylvanian of the Mississippi Valley as *Composita trilobata* which they considered to be specifically distinct from *C. trinuclea* (Hall) because of its larger size, although it is similar in every other respect to Hall's species. Size alone is not considered here to be of specific importance. Since Hall's species has priority, *Composita trilobata* Dunbar and Condra is here considered to be synonymous with *C. trinuclea*.

The collection contained 115 silicified specimens of this species.

Localities.— $\frac{3199}{19A}$, $\frac{43106}{19B}$.

Figured specimens.—U. Wyo. IT-221, IT-222.

Other specimens.—U. Wyo. IT-223, IT-224.

COMPOSITA sp.

The collections contained 104 specimens which were too poorly preserved to allow other than generic designation.

Localities.— $\frac{2997}{6A}$, $\frac{3199}{19A}$, $\frac{43106}{19B}$.

Specimens.—U. Wyo. IT-225-IT-227.

Genus CLEIOTHYRIDINA Buckman, 1906
CLEIOTHYRIDINA sp.
Plate 1, figure 15

The collections contain 15 specimens of this genus, all of which are too exfoliated or deformed to allow specific designation. The genus was identified by serial sections which showed the dorsal median septum and the posterior perforation of the dorsal hinge plate.

Localities.— $\frac{3099}{9A}$, $\frac{43106}{19A}$, $\frac{43106}{19B}$.

Figured specimens.—U. Wyo. IT-228.

Other specimens.—U. Wyo. IT-229, IT-230.

Genus EUMETRIA Hall, 1863

Genotype.—Retzia verneuilana Hall, 1856.

The shell is small or medium sized, subovate in outline, and moderately biconvex. The surface of both valves is marked by even, radial costae. The shell is commonly not sulcate, but there is a low ventral sulcus in advanced forms. There is no dorsal fold. The cardinal area contains very small interareas with the lateral margins abruptly

upturned. The shell matter is finely punctate.

Dental lamellae are lacking. The anterior and posterior parts of the dorsal hinge plate extend sharply in opposite directions. There are eight volutions in the spiralia. Muscle scars are unknown.

This is the only punctate spiriferoid with a subovate outline.

EUMETRIA SULCATA Burk, n. sp.
Plate 1, figures 31–34

The shell is medium sized, subovate in outline, and gently biconvex with the greatest convexity of both valves in the umbonal region. The greatest width is near the anterior of the shell. The surface of both valves is nearly always marked by 38 even, rounded costae. The ventral valve bears a broad, shallow sulcus at its anterior margin. The ventral beak is incurved, but not beyond the ventral interarea. The interareas are very small, and the delthyrium is almost entirely closed dorsally, but the pedicle aperture is large and round. The shell matter is very finely punctate.

This species is most similar to *Eumetria costata* (Hall), 1858, except for the presence of the ventral sulcus. No species of this genus have before been noted from Pennsylvanian rocks. *Eumetria sulcata*, therefore, represents a stratigraphically useful as well as easily recognizable species.

Locality.— $\frac{3199}{19A}$.

Holotype.—U. Wyo. IT-231.
Paratypes.—U. Wyo. IT-232.

Genus WELLERELLA Dunbar and Condra, 1932
WELLERELLA OSAGENSIS (Swallow)
Plate 1, figures 23–25

Rhynchonella (Camarophoria) osagensis SWALLOW, 1858, Acad. Sci. St. Louis Trans., vol. 1, p. 219, pl. 37, figs. 1–4.
Pugnax osagensis GIRTY, 1908, U. S. Geol. Survey Prof. Paper 58, pp. 317–318, pl. 24, figs. 16–16b.
Pugnoides osagensis GIRTY in Butler et al., 1920, U. S. Geol. Survey Prof. Paper 111, pl. 54, figs. 17–17a.
Wellerella osagensis DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, 2nd ser., pp. 288–289, pl. 37, figs. 1–4.

The shell is small, subglobular, typically rhynchonelloid in shape, and subtriangular to subpentagonal in outline, with the greatest width near the anterior margin of the shell. The dorsal fold and ventral sulcus are very prominent, especially at the anterior margin of the shell. The line of commissure is uniplicate and crenulate. The fold and sulcus normally contain two to four costae, with from 6–12 costae on each lateral slope. Ventrally curved crura extend from the anterior margin of an undivided, triangular dorsal hinge plate, which is supported by a short, simple median septum.

In erecting this species, Swallow (1858, pp. 219–220) states that "this species is very variable; some gibbous, others depressed; in some the length is greater than the breadth, while the reverse is true in others. The sinus varies in width and depth, and is marked with from two to six plications; all of the plications are usually more strongly marked in a gibbous specimen." It is in this broad sense that Swallow's species is accepted in this paper.

Localities.— $\frac{3099}{9B}$, $\frac{3199}{19A}$, $\frac{43106}{19B}$.

Figured specimen.—U. Wyo. IT-233.
Other specimens.—U. Wyo. IT-234-IT-236.

Phylum MOLLUSCA
Genus ALLORISMA King, 1844
ALLORISMA TERMINALE Hall
Plate 1, figures 38–40

Allorisma terminalis HALL in Stansbury, 1853, Exploration and Survey of the Valley of the Great Salt Lake of Utah. House Exec. Document 3, p. 413, pl. 2, figs. 4a–b.

The shell is medium sized, elongate and ovate, and generally highly inflated in the umbonal region of both valves. The posterior extremities are subangular. The surface of both valves is marked by wide concentric ridges which diverge from the beak and are most prominent near the center of the valves. There are also very fine concentric striae accompanying these larger ridges.

Four poorly preserved internal impressions of *Allorisma terminale* were collected at Locality $\frac{43106}{19B}$. In addition, the collection from Locality $\frac{3099}{9A}$ contains four speci-

mens which are possibly referable to this species. All are fragmentary and distorted, and are much smaller than is typical of the species, the largest being only 15 mm. from the posterior to the anterior margins. Otherwise they are all very similar to *A. terminale*.

Localities.— $\frac{3099}{9A}$, $\frac{43106}{19B}$.

Figured specimens.—U. Wyo. IT-237-IT-239.

Other specimens.—U. Wyo. IT-240, IT-241.

Genus NATICOPSIS M'Coy, 1842

NATICOPSIS sp.

A single specimen of this genus is present n the collection from Locality $\frac{3099}{19A}$. It is fragmentary and preserves only the apex and first three whorls of a naticiform shell of indeterminable size. Although the shell is exfoliated, there are indications of vertical striations.

Specimen.—U. Wyo. IT-242.

Goniatite

The collection from Locality $\frac{3199}{19A}$ contains a single, crushed, immature goniatite. The specimen was examined for Biggs by Dr. Walter Youngquist who did not give it a taxonomic designation. He said, however, that it suggests a late Mississippian form but that it is too immature to be diagnostic.

Specimen.—U. Wyo. IT-243.

Tetracoral

A single, badly weathered, distorted, fragmentary tetracoral was taken from Locality $\frac{2997}{6A}$.

Specimen.—U. Wyo. IT-244.

BIBLIOGRAPHY

BIGGS, C. A., 1951, Stratigraphy of the Amsden formation of the Wind River Range and adjacent areas in northwestern Wyoming: Unpublished Master's thesis on file at the University of Wyoming, Laramie, Wyoming.

BLACKWELDER, ELIOT, 1913, New or little known Paleozoic faunas from Wyoming and Idaho: Am. Jour. Sci., 4th ser., vol. 36, pp. 173–175.

MANUSCRIPT RECEIVED MARCH 16, 1953

——, 1918, New geologic formations in western Wyoming: Washington Acad. Sci. Jour., vol. 8, pp. 417–426.

BRANSON, C. C., 1937, Stratigraphy and fauna of the Sacajawea formation, Mississippian, of Wyoming: Jour. Paleontology, vol. 11, pp. 650–660, pl. 89.

——, 1939, Pennsylvanian formations of central Wyoming: Geol. Soc. America Bull., vol. 50, pp. 1199–1226, 3 pls.

BRANSON, E. B., and GREGER, D. K., 1918, The Amsden formation of the east slope of the Wind River Mountains of Wyoming and its fauna: Geol. Soc. America Bull., vol. 29, pp. 309–326, pls. 18, 19, 1 text fig.

CLOUD, P. E., 1942, Terebratuloid Brachiopoda of the Silurian and Devonian: Geol. Soc. America Spec. Pap. 38, xi+182 pp., 26 pls., 17 text figs., 3 tables.

DARTON, N. H., 1904, Comparison of the stratigraphy of the Black Hills, Bighorn Mountains, and the Rocky Mountain Front Range: Geol. Soc. America Bull., vol. 15, pp. 379–448, pls. 23–36.

——, 1906, Geology of the Bighorn Mountains: U. S. Geol. Survey Prof. Paper 51, 443 pp., 72 pls., 14 text figs.

——, 1908, Paleozoic and Mesozoic of central Wyoming: Geol. Soc. America Bull., vol. 19, pp. 403–470, pls. 21–30.

DUNBAR, C. O., and CONDRA, G. E., 1932, Brachiopoda of the Pennsylvanian system of Nebraska: Nebraska Geol. Survey Bull. 5, 2d ser., 377 pp., 44 pls., 25 text figs., 4 tables, 1 range chart.

LEE, W. T., 1927, Correlation of the geologic formations between east-central Colorado, central Wyoming, and southern Montana: U. S. Geol. Survey Prof. Paper 149, v+10 pp., 34 pls., 5 text figs.

LOVE, J. D., 1939, Geology along the southern margin of the Absaroka Range, Wyoming: Geol. Soc. America Spec. Pap. 20, vii+134 pp., 17 pls., 3 text figs.

MOORE, R. C., et al., 1944, Correlation of the Pennsylvanian formations of North America: Geol. Soc. America Bull., vol. 55, pp. 657–706, 1 pl.

MOREY, P. S., 1935, Ostracoda from the Amsden formation of Wyoming: Jour. Paleontology, vol. 9, pp. 474–482, pl. 54.

SCOTT, H. W., 1935, Some Carboniferous stratigraphy in Montana and northeastern Wyoming: Jour. Geology, vol. 43, pp. 1011–1032, 3 text figs., 6 tables.

WILLIAMS, J. S., 1948, Mississippian-Pennsylvanian boundary problems in the Rocky Mountain region: Geol. Soc. America Bull., vol. 56, pp. 327–351, 2 text figs.

WELLER, J. M., et al., 1948, Correlation of the Mississippian formations of North America: Geol. Soc. America Bull., vol. 59, pp. 91–196, 2 pls., 7 text figs.

WELLER, STUART, 1914, The Mississippian Brachiopoda of the Mississippi Valley Basin: Illinois Geol. Survey Mon. 1, 508 pp., 83 pls., 36 text figs.

EXPLANATION OF PLATE 1

FIG. *1—Orthotetes?* sp. Unique specimen from Loc. $\frac{43106}{19B}$. ×1. U. Wyo. IT-187. (p. 9)

2–4, 11—Composita subtilita (Hall) var. *ovata* Mather. *2, 4.* Dorsal and lateral views showing shape and line of commissure. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-215. *3.* Anterior view showing line of commissure. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-216. *11.* Dorsal view showing shape of larger specimen. Loc. $\frac{43106}{19B}$. U. Wyo. IT-217. (p. 12)

5–7, 12—Composita subtilita (Hall) var. *subtilita. 5.* Dorsal view showing general shape. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-211. *6, 7.* Anterior and lateral views showing shape, line of commissure, and lamellose growth lines. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-212. *12.* Same specimen. ×2. U. Wyo. IT-212. (p. 12)

8–10—Composita subtilita (Hall) var. *trinuclea* (Hall). *8.* Dorsal view showing shape. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-221. *9, 10.* Anterior and lateral views showing shape and line of commissure. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-222. (p. 13)

13, 14—Lingulodiscina sp. *13.* Dorsal view of immature specimen. Loc. $\frac{3099}{9B}$. ×2. U. Wyo. IT-184. *14.* Dorsal view of mature specimen. Loc. $\frac{3099}{9B}$. ×1. U. Wyo. IT-185. (p. 8)

15—Cleiothyridina sp. Dorsal view of exfoliated specimen showing shape and median septum. Loc. $\frac{43106}{19A}$. ×1. U. Wyo. IT-228. (p. 13)

16–22—Spirifer opimus Hall. *16.* Dorsal view showing arrangement of costae. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-202. *17, 18.* Ventral and dorsal views showing shape and arrangement of costae. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-294. *19.* Posterior view of steinkern showing dental lamellae and striated interareas. Loc. $\frac{3099}{LA}$. ×2. U. Wyo. IT-201. *20.* Postero-ventral, showing sulcus and costae on ventral beak. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-203. *21, 22.* Anterior and lateral views showing shape and line of commissure. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-205. (p. 11)

23–25—Wellerella osagensis (Swallow). Dorsal, anterior, and lateral views showing shape and prominent fold and sulcus. Loc. $\frac{3199}{19A}$. ×2. U. Wyo. IT-233. (p. 14)

26–28—Marginifera muricatina Dunbar & Condra. *26.* Posterior view of trail showing coarse costae and spine bases. Loc. $\frac{3099}{9A}$. ×1. U. Wyo. IT-197. *27, 28.* Posterior and dorsal views showing shape and ornamentation. Loc. $\frac{3099}{9A}$. ×1. U. Wyo. IT-198. (p. 10)

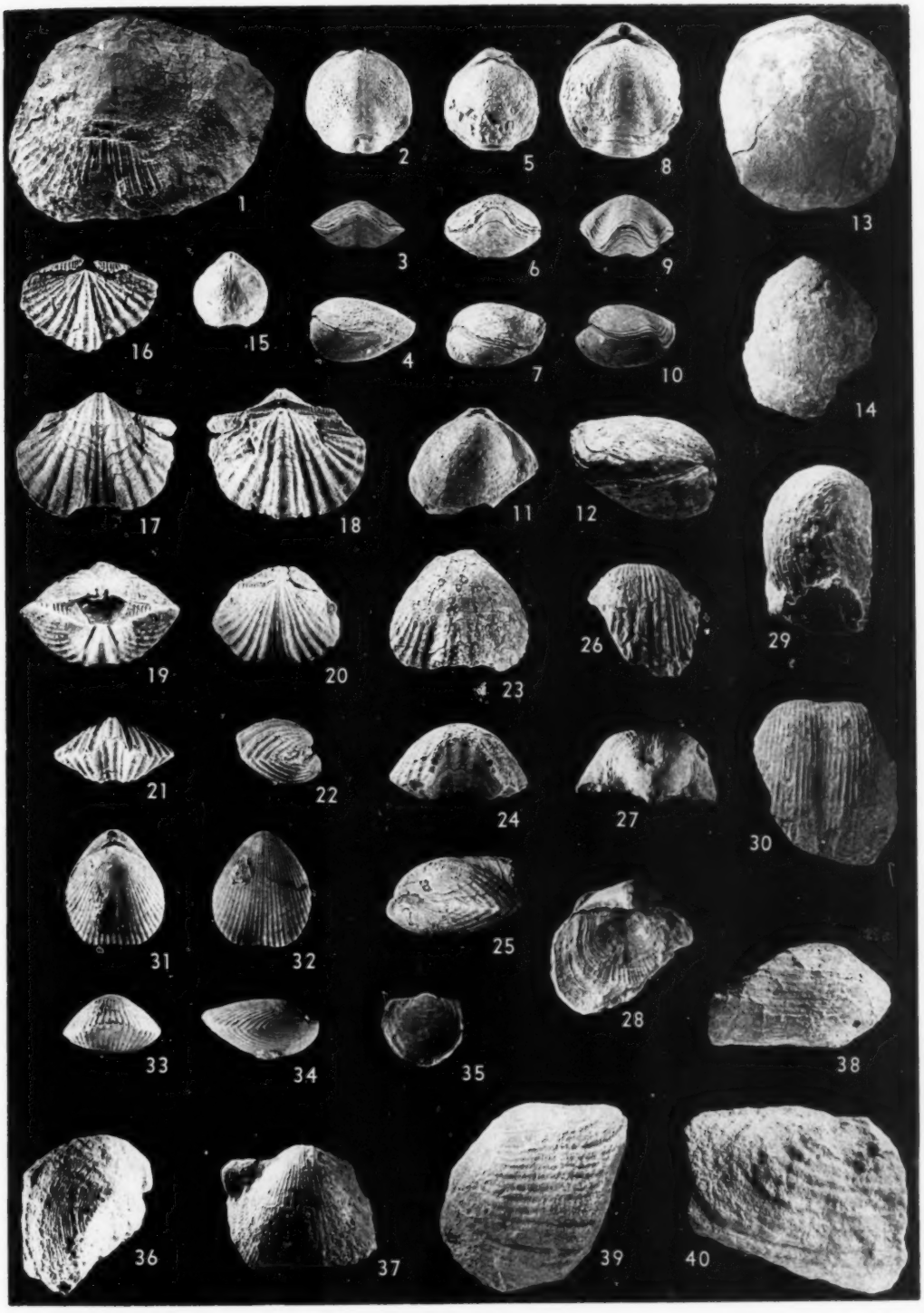
29, 30—Dictyoclostus portlockianus (Norwood & Pratten). *29.* Lateral view showing general shape. Loc. $\frac{43106}{19B}$. ×1. U. Wyo. IT-189. *30.* Anterior view showing ribbing and sulcus on trail. Loc. $\frac{43106}{19B}$. ×1. U. Wyo. IT-188. (p. 9)

31–34—Eumetria sulcata Burk, n. sp. Dorsal, ventral, anterior, and lateral views of holotype. Loc. $\frac{3199}{19A}$. ×1. U. Wyo. IT-231. (p. 14)

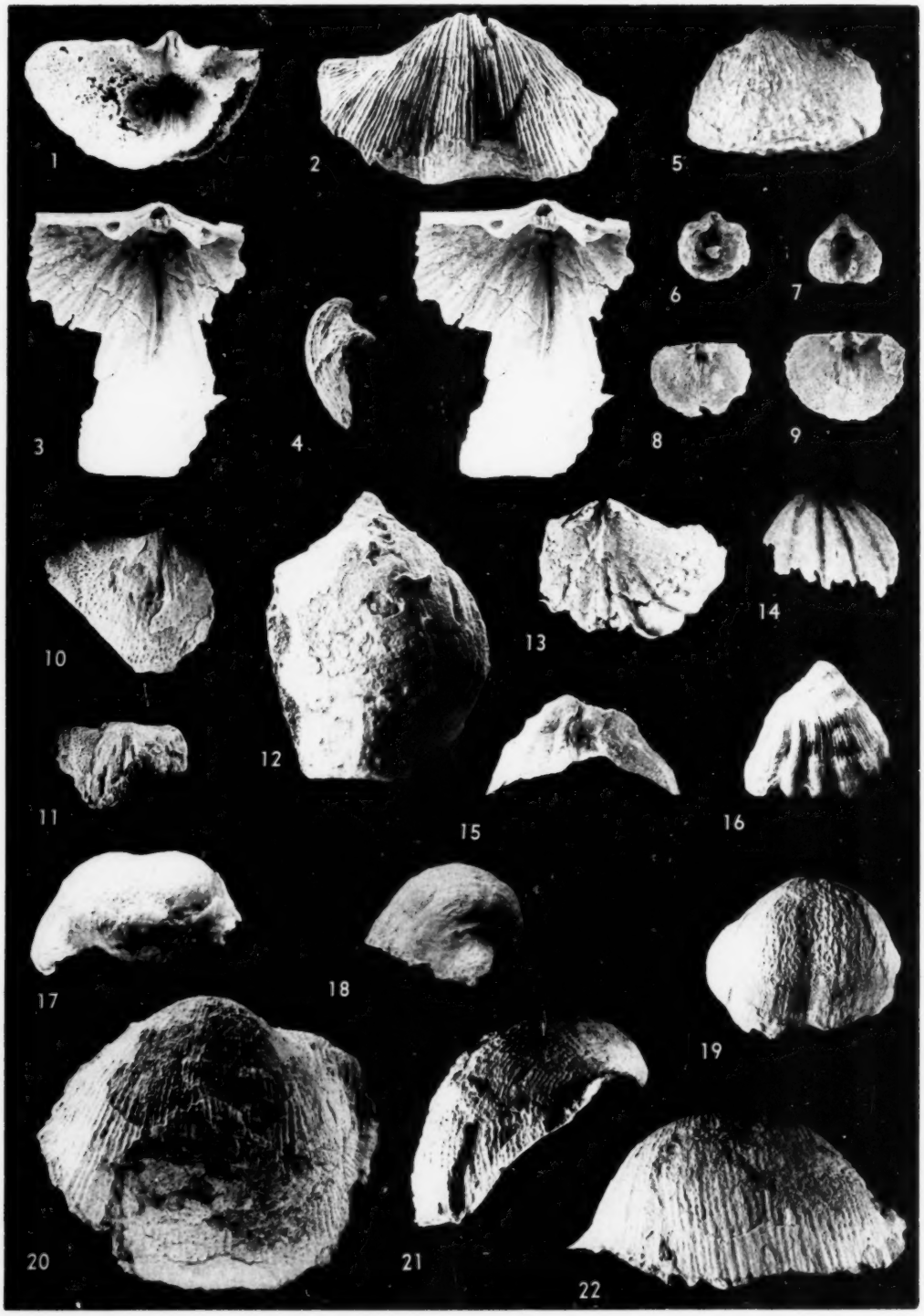
35—Cancrinella boonensis (Swallow). External impression of ventral valve, reverse-lighted, showing concentric rugae on umbo, and spine bases on cardinal extremities. Loc. $\frac{3099}{9A}$. ×2. U. Wyo. IT–195. (p. 10)

36, 37—Linoproductus prattenianus (Norwood in Norwood & Pratten). *36.* Lateral view showing shape and costae. Loc. $\frac{43106}{19B}$. ×1. U. Wyo. IT-192. *37.* View of ventral beak showing prominent wrinkled cardinal extremities. Loc. $\frac{43106}{19B}$. ×2. U. Wyo. IT-193. (p. 9)

38–40—Allorisma terminale Hall. *38.* Small specimen referred to this species with hesitation. Loc. $\frac{3099}{9A}$. ×2. U. Wyo. IT-237. *39.* Left valve. Loc. $\frac{43106}{19B}$. ×1. U. Wyo. IT-238. *40.* Right valve showing concentric ornamentation. Loc. $\frac{43106}{19B}$. ×1. U. Wyo. IT-239. (p. 14)



Burk, Amsden fauna



Pederson, Casper fauna

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 17–21, PL. 2, JANUARY, 1954

A PERMIAN (WOLFCAMPIAN) FAUNA OF THE CASPER FORMATION OF SOUTHEASTERN WYOMING

SELMER L. PEDERSON
Box 1589, Durango, Colorado

ABSTRACT—A new subspecies of *Neospirifer* was found in a bed 415 feet above the base of the Casper formation near Laramie, Wyoming. A complete description of the new subspecies, *N. bakeri wyomingensis*, is included.

The other genera in the fauna which marks the base of the Permian in the Laramie Range are *Dictyoclostus*, *Juresania*, *Marginifera*, *Meekella*, *Chonetes*, *Wellerella*, and *Composita*, which is the dominant genus.

INTRODUCTION

THE purpose of this paper is to describe a fauna which marks the base of the Permian part of the Casper formation in the Laramie Range near Laramie, Wyoming. This fauna includes a new subspecies. *Neospirifer bakeri wyomingensis* Pederson.

ACKNOWLEDGEMENT

I wish to express my sincere thanks to Dr. Alan B. Shaw, of the Department of Geology, University of Wyoming, for his guidance in preparing the manuscript. Thanks are due to Dr. Horace D. Thomas, of the Department of Geology, University of Wyoming, for critically reading the manuscript. I would also like to acknowledge that the Wyoming Geological Survey supplied film for the pictures on the accompanying plate.

STRATIGRAPHY

The fauna described below was discovered in NW ¼, Sec. 4, T. 16 N., R. 72 W., Sixth Principal Meridian, about 8 miles northeast of Laramie on the Ninth Street road, and is on the ridge above the University of Wyoming stone quarry. The locality

EXPLANATION OF PLATE 2

All specimens are from 415 feet above the base of the Casper formation in NW¼, Sec. 4, T. 16 N. R. 72 W., Albany Co., Wyoming.

FIGS. *1–4—Neospirifer bakeri* (King), *wyomingensis* Pederson, n. subsp. *1.* Holotype. Interior of silicified ventral valve showing absence of dental plates. ×2. U. Wyo. IT-153. *2.* Paratype. Exterior of ventral valve showing low round radial plications and shallow sulcus. ×1. U. Wyo. IT-155. *3.* Paratype. Stereoscopic pair. Interior of silicified dorsal valve showing prominent dental sockets and gaping notothyrium. ×2. U. Wyo. IT-154. *4.* Paratype. Lateral view showing the short simple beak. ×1. U. Wyo. IT-156. (p. 18)

5—Juresania nebrascensis (Owen). Ventral valve showing quadrangular shape and pustulose spine bases. ×2. U. Wyo. IT-170. (p. 20)

6–9—Composita ovata Mather. *6, 7.* Silicified ventral valves. ×2½. U. Wyo. IT-158 b, a. *8, 9.* Silicified dorsal valves. ×2½. U. Wyo. IT-159 a, b. (p. 19)

10–11—Chonetes sp. indet. *10.* Ventral view showing the even radial rows of internal pustules. ×2. U. Wyo. IT-166. *11.* Internal impression of ventral valve showing muscle scars. ×1. U. Wyo. IT-165. (p. 20)

12—Composita subtilita (Hall). Dorsal view showing the sub-ovate outline and narrow beak. ×2. U. Wyo. IT-161. (p. 19)

13–14—Wellerella sp. indet. *13.* Interior of silicified dorsal valve showing median septum. ×2½. U. Wyo. IT-175. *14.* Exterior of silicified dorsal valve showing the plications. ×2. U. Wyo. IT-174. (p. 21)

15–16—Meekella attenuata Girty. *15.* Inverted posterior view of ventral valve showing the large triangular cardinal area. ×2½. U. Wyo. IT-162. *16.* Ventral view of ventral valve showing the fine radial lirae on broad, flattened plications. ×2. U. Wyo. IT-162. (p. 20)

17–19—Marginifera haydenensis Girty. *17.* Posterior view showing small dorsally deflected ears. ×2. U. Wyo. IT-172. *18.* Lateral view. ×2. U. Wyo. IT-172. *19.* Ventral view showing shallow mesial sinus. ×2. U. Wyo. IT-172. (p. 21)

20–22—Dictyoclostus americanus Dunbar & Condra. *20.* Ventral view showing costate ribbing. ×1. U. Wyo. IT-168. *21.* Lateral view. ×1. U. Wyo. IT-168. *22.* Anterior view showing ribbing. ×1. U. Wyo. IT-168. (p. 20)

is numbered $\frac{1672}{4A}$ in the University of Wyoming files.

The Casper formation is approximately 800 feet thick at this locality, consisting of interfingering arkosic grits, cross-laminated sandstones, and fossiliferous limestones. In the Laramie Basin region this sequence is the oldest sedimentary unit and is in contact with the pre-Cambrian Sherman granite below and the Permian Satanka red shale above (Miller and Thomas, 1936, p. 718; Thomas, 1949, p. 17).

The fauna was found in an eight-inch lavender silicified limestone at the top of a ten foot bed of massive, brown limestone bearing *Triticites*. The lavender bed lies approximately 415 feet above the granite but irregularities on the surface of the granite make this estimate subject to variation; Thompson and Thomas in an unpublished manuscript give the height above the granite as 390 feet. The collection from this bed is of Permian age, but a fauna collected and identified by Mr. Creighton A. Burk (unpublished) from a bed 10 feet lower is Pennsylvanian. Therefore, the fauna discussed here marks the base of the Permian within the Casper formation.

The silicified limestone contains few brachiopods that can be broken out, but silicified specimens are well preserved and were freed by etching in hydrochloric acid.

The fauna includes the following: *Dictyoclostus americanus* Dunbar and Condra, 1932 (4 specimens); *Juresania nebrascensis* (Owen), 1852 (1); *Marginifera haydenensis* Girty, 1903 (16); *Meekella attenuata* Girty, 1908 (13); *Chonetes* sp. indet. (12); *Wellerella* sp. indet. (3); *Composita ovata* Mather, 1915 (467); *C. subtilita* (Hall in Stansbury), 1853 (1); *Neospirifer bakeri wyomingensis* Pederson, n. subsp. (39); Unidentified specimens (3). Dr. H. D. Thomas (personal communication, Nov. 18, 1952) states that fusulinids from this bed have been identified by M. L. Thompson as *Triticites ventricosus* (Meek) 1852?, a Wolfcampian type.

SYSTEMATIC PALEONTOLOGY

Phylum Brachiopoda

Genus Neospirifer Fredericks, 1919

Spirifer (*Neospirifer*) King, 1930, Univ. Texas Bull. 3042, p. 115.

Neospirifer Dunbar & Condra, 1932, Nebraska Geol. Survey Bull. 5, ser. 2, pp. 326–328.

Neospirifer Cooper in Shimer & Shrock, 1944, Index Fossils of North America, p. 325, John Wiley.

Diagnosis.—The shell of the genus *Neospirifer* is characteristically large and transverse with fasciculate costae.

The shell is widest at the hinge line and subtriangular in outline. The cardinal area of the ventral valve is moderately deep and wide, and the ventral beak arches up over it. The dorsal valve has a fold with a coinciding sulcus on the ventral valve. The fasciculate surface is formed by plications which bifurcate on the younger part of the shell. The fascicles may extend to the margins or degenerate into normal costae before reaching the anterior margin. On the well-preserved parts of the shell fine concentric lines are visible crossing delicately sculptured radial lirae.

Internally, the crural plates are fused to the heavy socket plates in the dorsal valve. The muscle scars of the pedicle valve are commonly divided by a median ridge. The shell is generally thickened in the umbonal region. The dental plates are long and conical, and may extend to the floor of the valve.

Neospirifer bakeri wyomingensis Pederson, n. subsp.

Plate 2, figures 1–4

Diagnosis.—This subspecies is characterized by an alate shape with a short ventral beak. It has a high fold on the dorsal valve and a low shallow sulcus on the ventral valve. It has strongly impressed muscle scars and a low median ridge. Dental lamellae are absent.

Description.—The shell is large with adult specimens measuring up to 53 mm. across the hinge and averaging 30 mm. long. The outer surface is covered by low, round, radial plications that remain low. On the dorsal valve the plications are bundled slightly on the posterior margin of the valve, but become indistinct anteriorly. On the ventral valve the bundling of the ribs is inconspicuous (fig. 2).

The ventral valve has a strongly developed apical callosity and the muscle scars are strongly impressed and are separated by a low median ridge (fig. 1). The

interareas are well developed with a wide delthyrium which has very small deltidial plates. The dental lamellae are absent (fig. 1).

The dorsal valve has prominent dental sockets and a gaping notothyrium (fig. 3). The interareas are high and subtriangular. The hinge teeth are supported by crural plates which are fused to the interareas.

Remarks.—The new subspecies most closely resembles *Neospirifer bakeri bakeri* (King) 1930. *N. bakeri bakeri* has short dental lamellae while *N. bakeri wyomingensis* has none. The muscle scars are invisible in *N. bakeri bakeri*, but are strongly impressed, with a low median ridge in *N. bakeri wyomingensis*. The dorsal fold of *N. bakeri bakeri* is low and the ventral sulcus is broad with a sharp ridge rising on each side while in *N. bakeri wyomingensis* the fold is high and the sulcus is low and narrow.

These differences, particularly regarding the dental lamellae, seem to warrant separation of the Casper form from *N. bakeri bakeri*, s.s., but because of the overall similarity of the Wyoming and Texas shells, the erection of a full species does not seem to be justified.

Comparison with other species.—The short simple beak and absence of dental lamellae distinguish *N. bakeri wyomingensis* from *N. dunbari*, *N. costella*, *N. pseudocameratus*, and *N. mexicanus* var. *latus*, all of which have incurved beaks and well-developed dental lamellae. The short simple beak and alate hinge distinguish *N. bakeri wyomingensis* from *N. huecoensis* which has a strongly incurved beak and a transversely elliptical, short-hinged shape. *N. costella*, *N. dunbari*, and *N. mexicanus* var. *latus* also have elliptical to subtriangular shapes.

Holotype.—U. Wyo. IT-153.

Paratypes.—U. Wyo. IT-154–157, 164.

Genus COMPOSITA Brown, 1849
COMPOSITA OVATA Mather, 1915
Plate 2, figures 6–9

Composita ovata MATHER, 1915, Denison Univ. Sci. Lab. Bull., vol. 18, p. 202, pl. 14, figs. 6–6c.

Composita ovata DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, ser. 2, pp. 370–371, pl. 43, figs. 14–19.

The shell is medium sized with a convex ventral valve which is oval in outline. The delthyrium of the ventral valve is concealed by the upward curving of the beak. The sinus originates in the umbonal region and extends to the marginal edge of the valve and is shallow. The dorsal valve has a low broad fold. The surface of both valves is covered by fine concentric lines of growth, which are commonly crossed by fine thread-like radial striae.

The dorsal valve has a well-developed brachial apparatus. The dental sockets are supported by crural plates that form the inner sides of the sockets. A pair of ventrally curved processes arise from the front of the hinge-line. These serve as a base for the primary lamellae of the spiralia. The adductor scars are long and narrow and lightly impressed on the dorsal valve.

Figured specimens.—U. Wyo. IT-158 a, b, 159 a, b.

Other specimens.—U. Wyo. IT-160.

COMPOSITA SUBTILITA (Hall in Stansbury), 1853
Plate 2, figure 12

Terebratula subtilita HALL in Stansbury, 1853, Exploration and survey of the valley of the Great Salt Lake, Utah, Appendix E, p. 490, pl. 4, figs. 1a–2c.

Seminula subtilita GIRTY, 1903, U. S. Geol. Survey Prof. Paper 16, pp. 403–407, pl. 7. figs. 1–10.

Composita subtilita GIRTY, 1915, U. S. Geol. Survey Bull. 544, pp. 96–101, pl. 5, fig. 7; pl. 6, fig. 13; pl. 12, figs. 4–4c.

Composita subtilita DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, ser. 2, pp. 363–366, pl. 43, figs. 7–13.

Composita subtilita COOPER in Shimer & Shrock, 1944, Index Fossils of North America, p. 335, pl. 128, figs. 9–12, John Wiley.

The shell is large and subovate in outline. It has a narrow beak while the anterior part is broadly rounded. The delthyrium is hidden by the close incurvature of the beak. The hinge-line is not visible but is short and without a cardinal area. A broad, rounded ventral sinus and corresponding dorsal fold mark the anterior half of the shell. The surface is smooth except for very fine growth lines.

Compared with *C. ovata*, *C. subtilita* is larger and has a narrow beak which hides the hinge-line completely. *C. subtilita* has a broad, deep, rounded ventral sinus and correspondingly high dorsal fold while *C. ovata* has a broad, shallow ventral sinus and a low dorsal fold.

Figured specimen.—U. Wyo. IT-161.

Genus MEEKELLA White & St. John, 1867

MEEKELLA ATTENUATA Girty, 1908

Plate 2, figures 15, 16

Meekella attenuata GIRTY, 1908, U. S. Geol. Survey Prof. Paper 58, pp. 205–208, pl. 24, figs. 7–9a; pl. 25, figs. 4–4d.

Meekella attenuata KING, 1930, Univ. Texas Bull. 3042, pp. 52–53, pl. 5, figs. 2–7.

The shell is small. The ventral valve has an irregularly convex shape with the hinge width equal to half the shell width. The deltidium is narrow with the lateral parts rising with concave slopes to a narrow and subangular median ridge (fig. 15). There are seven to ten fine ribs on each of the eight plications, which become indistinct towards the beak, leaving a small unplicated region (fig. 16).

The dorsal valve is subcircular in outline and strongly convex. It has a faint mesial sinus and no cardinal area. The surface has fine radial lirae on plications which are broader and flatter than those on the ventral valve. The dorsal plications arise gradually, some distance from the beak as on the ventral valve. Faint concentric lines cross the lirae and produce the characteristic orthotetid surface.

This species may be distinguished from *M. striatocostata* (Cox) 1857, which is also common in the Casper formation, by the attenuation of the ribbing posteriorly. In *M. striatocostata* the ribs are well defined on the umbo; in *M. attenuata* they are not.

Figured specimens.—U. Wyo. IT-162.

Other specimens.—U. Wyo. IT-163, 164.

Genus CHONETES Fischer, 1830–37

CHONETES sp. indet.

Plate 2, figures 10, 11

The ventral valves are only half as long as they are wide. The greatest width is at the hinge-line. The outline of the specimens is distinctly subquadrate, since the lateral margins are converging only slightly. The beak on the ventral valve is fairly prominent and the valve is gently convex and has a moderate sulcus, which distinguishes it from *C. granulifera*. The surface of the valve has fine capillate ornamentation.

The cardinal areas are rather narrow and taper gradually from the delthyrium to the cardinal extremities. Normally there are seven to eight spines on each side of the cardinal area. Markings caused by the fine papillae found on the inside of the shell may be seen in exfoliated specimens (fig. 10).

Figured specimens.—U. Wyo. IT-165, 166.

Other specimens.—U. Wyo. IT-167.

Genus DICTYOCLOSTUS Muir-Wood, 1930

DICTYOCLOSTUS AMERICANUS Dunbar & Condra, 1932

Plate 2, figures 20–22

Dictyoclostus americanus DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, ser. 2, pp. 218–220, pl. 34, figs. 3–6.

Dictyoclostus americanus COOPER in Shimer & Shrock, 1944, Index Fossils of North America, p. 350, pl. 136, figs. 15–19, John Wiley.

The shell is large with a breadth of 5.0 cm. and a length of 4.2 cm., and is strongly concavo-convex. The hinge width is nearly the same as the greatest width of the shell. The ventral umbo is broad and only moderately convex. The ears are arched and small. The beak is small and obtuse. The surface has costate ribbing crossed by regular concentric rugae of equal thickness to form an even-textured reticulate pattern. The dorsal valve is moderately concave, and the shell has a moderate trail. The ventral valve bears a large number of slender spines which are irregularly distributed over the surface while the dorsal valve bears no spines.

This species may be distinguished from *D. portlockianus* (Norwood and Pratten), 1854, which is common in the Pennsylvanian parts of the Casper, by its ribbing, which is very fine over the visceral disc but becomes coarser and unequal on the anterior slope; in *D. americanus* the ribbing remains even-textured.

Genus JURESANIA Fredericks, 1928

JURESANIA NEBRASCENSIS (Owen), 1852(?)

Plate 2, figure 5

Productus nebrascensis MEEK, 1872, U. S. Geol. Survey Nebraska Final Rept., pt. 2, pp. 165–167, pl. 2, fig. 2; pl. 4, fig. 6; pl. 5, figs. 11a–c.

Productus nebraskensis GIRTY, 1903, U. S. Geol. Survey Prof. Paper 16, pp. 370–371, pl. 5, figs. 1–2, 2a.

Productus nebrascensis GIRTY, 1904, U. S. Geol. Survey Prof. Paper 21, p. 53, pl. 11, figs. 7–9.
Productus nebrascensis GIRTY, 1909, U. S. Geol. Survey Bull. 389, pp. 62–64, pl. 7, figs. 5–6.
Productus nebrascensis GIRTY, 1915 (part), U. S. Geol. Survey Bull. 544, pp. 65–68, pl. 10, figs. 6–7.
Juresania nebrascensis DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, ser. 2, pp. 195–198, pl. 22, figs. 1–9, 13.
Juresania nebrascensis COOPER in Shimer & Shrock, 1944, Index Fossils of North America, p. 350, pl. 137, figs. 1–3, John Wiley.

The shell is small, with a width of 17 mm. and a length of 11 mm. It has moderate costae which are crossed by concentric bands upon which the spines are borne. The spines pass through the shell material at a low angle and emerge at a tangent to the surface, from prominent, elongate, pustulose spine bases (fig. 5).

The ventral valve is strongly convex and geniculate. It has a distinct quadrangular shape, and the hinge-line is not as wide as the greatest width. The ears are small and the beak overarches the hinge-line. The dorsal valve is nearly flat over the visceral area becoming curved up towards the margins so as to make it moderately convex.

Figured specimen.—U. Wyo. IT-170.
Other specimens.—U. Wyo. IT-171.

Genus MARGINIFERA Waagen, 1884

MARGINIFERA HAYDENENSIS Girty, 1903

Plate 2, figures 17–19

Marginifera haydenensis GIRTY, 1903, U. S. Geol. Survey Prof. Paper 16, pp. 380–381, pl. 5, figs. 9–11a.
Marginifera haydenensis DUNBAR & CONDRA, 1932, Nebraska Geol. Survey Bull. 5, ser. 2, pp. 232–234, pl. 36, figs. 12–17.

The shell is small, with a length of 12 mm. and a width of 17 mm. The ventral valve is strongly convex (fig. 18). The ventral valve has a shallow, moderate mesial sinus (figs. 17, 19). The submarginal ridges are exaggerated on both valves. The vault of the shell is usually large. The surface is marked by fine irregular longitudinal striae, and spines are commonly abundant. The dorsal valve is transverse and much smaller than the ventral valve. The only ornamentation found on the dorsal valve consists of concentric wrinkles or fine striae.

Figured specimens.—U. Wyo. IT-172.
Other specimens.—U. Wyo. IT-173.

Genus WELLERELLA Dunbar & Condra, 1932

WELLERELLA sp. indet.

Plate 2, figures 13, 14

The dorsal valve is convex and smooth on the umbo. Plications start 3 or 4 mm. from the beak of the dorsal valve. There is also a narrow sinus on the fold of the dorsal valve. There are three plications on the fold and three on each lateral slope. Internally the specimens show a dorsal median septum.

None of the specimens is well enough preserved to permit more than generic identification.

Figured specimens.—U. Wyo. IT-174, 175.
Other specimens.—U. Wyo. IT-176.

MANUSCRIPT RECEIVED MARCH 16, 1953

REFERENCES

MILLER, A. K., and THOMAS, H. D., 1936, The Casper formation of Wyoming and its cephalopod fauna: Jour. Paleontology, vol. 10, pp. 715–738, pls. 96–99, 4 text-figs.
THOMAS, H. D., 1949, The geological history and geological structure of Wyoming: Wyoming Geol. Survey Bull. 42, pp. 1–28, 17 text-figs.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 22–25, 2 TEXT FIGS., JANUARY 1954

GROWTH AND DECLINE OF POPULATIONS AND THE DISTRIBUTION OF MARINE PELECYPODS

DAVID NICOL
U. S. National Museum

ABSTRACT—A study of the geologic and geographic histories of 20 species of late Cenozoic pelecypods has shown me that there is a direct relationship between the increase of numbers of a species and its increase in geographic distribution.

INTRODUCTION

THE ideas presented in this paper are the result of observations on morphology, taxonomic relationship, geologic range, and geographic range of 20 species of late Cenozoic pelecypods. These species are found in Miocene or younger beds ranging from New Jersey to Florida; they include short-lived endemic species and long-lived wide-spread ones. In an earlier study of mine (1953c) on the period of existence of these same species, I noted that the longer-lived ones generally had greater numbers of individuals, greater variability of shell morphology, and a wider geographic distribution than the shorter-lived species.

GROWTH FORM OF POPULATIONS

While reading Chapter 21 in Allee et al. (1949, pp. 305–330), I realized that the history of a species, its growth in numbers and geographic distribution, is like that of the history of a population. This is to be expected, inasmuch as a species consists of one or more populations. This startling similarity is particularly well shown in long-lived widely-distributed species. On page 264 Allee et al. make the following statement:

> Another such character concerns numerical distribution in space and in time—dispersion. The geographic position of an individual organism is hardly a matter of much import. But the dispersion of its group may, and usually does, have great significance both in terms of survival of the group and of its impact on the environment it exploits. Thus dispersion emerges as a population attribute.

On pages 305–306 Allee et al. list the stages of population growth. A condensed and somewhat modified account of this outline is as follows:

I. The period of positive, sigmoid growth (the population increasing).
   A. The establishment of the population.
   B. The period of rapid growth (sometimes called the logarithmic phase).
   C. The period of decreased growth rate as the asymptote is approached.
II. The equilibrium position. (This phase consists of minor oscillations or fluctuations.)
III. The period of negative growth (population decline or contraction); consistent and progressive reduction of the population below equilibrium or below the lower range of usual fluctuations and/or oscillations.
IV. Extinction.

This outline is as applicable to species as it is to populations. However, these stages can be distinguished in only the long-lived species. Figure 1 (reproduced from Allee et al., p. 306, fig. 96) shows this outline in graphic form.

GROWTH FORM OF SPECIES

Detailed studies have been made on four species—*Euloxa latisulcata*, *Glycymeris aberrans*, *Glycymeris americana*, and *Anadara* (*Rasia*) *lienosa*. The first two species are short-lived and restricted in their distribution.

In a paper on *Euloxa latisulcata* (1953a) I made the following statement:

> In order to have migration and expansion of a species, the population or populations making up the species must increase in size; otherwise any considerable amount of migration and expansion of the geographic range of the species is impossible.

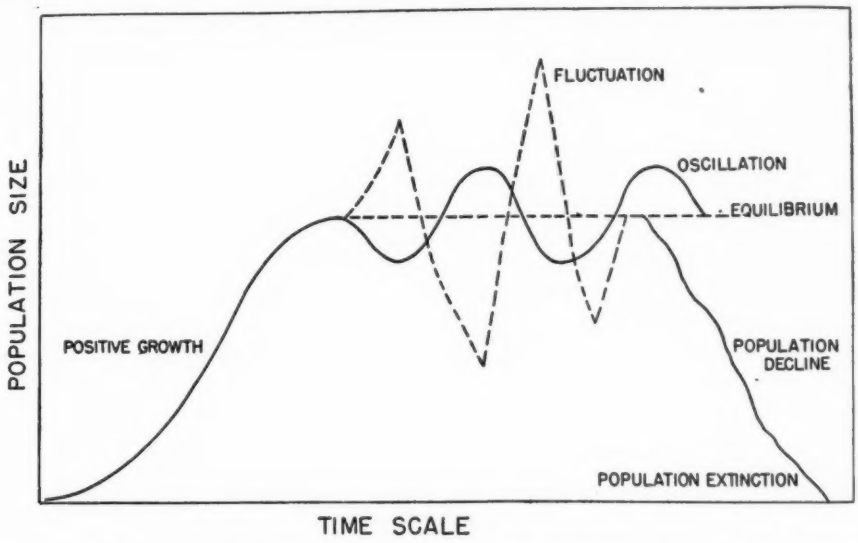


FIG. 1—Stylized representation of the various phases of population growth form (from Allee et al., 1949, p. 306, fig. 96, by permission of the author).

This statement contains the basic idea presented in this paper, as will be shown later.

Euloxa latisulcata has been reported from four localities in the St. Marys formation in Virginia. This same formation is well exposed in southern Maryland, but the species has never been reported from that state. I know of only ten specimens of this rare species. Thus, in a short-lived endemic species like *Euloxa latisulcata*, the three stages (growth, equilibrium, and decline) are not distinguishable.

Glycymeris aberrans has been reported from only two localities in South Carolina and Florida. This late Miocene glycymerid species is much rarer, has less variation in shell morphology, and has a much more restricted geographic distribution than its long-lived ancestor, *Glycymeris americana*.

Glycymeris americana and *Anadara* (*Rasia*) *lienosa* are long-lived and relatively widespread and variable species. A detailed study of their geologic and geographic ranges led to the idea that increase in numbers of individuals (i.e., the growth or increase of populations) of a species is closely related to the expansion of geographic range of that species.

The history of the geographic distribution of *Glycymeris americana* is typical of a long-lived species. The earliest known occurrence is in the late Miocene Yorktown formation of Virginia. Later in the Miocene, *Glycymeris americana* expanded rapidly in both numbers and range, reaching at least as far south as Florida. During this period of expansion, it became more variable in shell morphology and is an abundant species in all the late Miocene formations from Virginia to Florida. At the beginning of the Pliocene epoch the species contracted slightly, becoming extinct north of Cape Hatteras, but it was still an abundant species in the south. Toward the end of the Pliocene a definite decline in numbers of individuals and variability became apparent. In the Quaternary period *Glycymeris americana* is poorly represented; it is spotty in its distribution, and today it appears to be near extinction. Although living specimens have been found as far north as Cape Hatteras, large specimens are most commonly found in Florida, around Cape Canaveral and from Cedar Keys to Destin. A generalized graph of the distributional history and abundance of *Glycymeris americana* is shown in Figure 2.

Anadara (*Rasia*) *lienosa* was widespread and abundant in the late Miocene and has been found in beds of this age as far north as southern Virginia. During the Pliocene it was still abundant, and lived as far north as

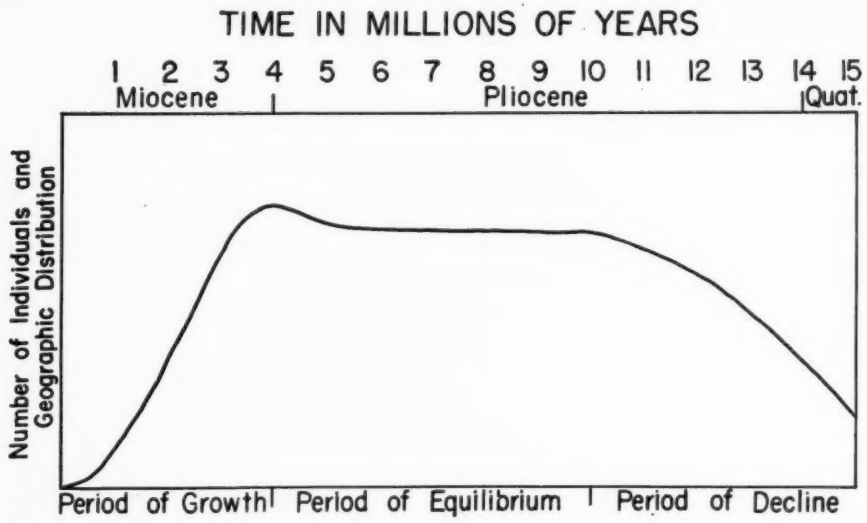

TIME IN MILLIONS OF YEARS
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Miocene
Pliocene
Quat.
Number of Individuals and Geographic Distribution
Period of Growth
Period of Equilibrium
Period of Decline

FIG. 2—Graph of the geologic and geographic history of *Glycymeris americana* (Defrance).

Cape Hatteras. Today, however, it is confined to Florida and a part of the Caribbean area. Its distributional history is much like that of *Glycymeris americana*, although its range is farther south,

The percentage of time in the period of existence of a species that is taken up by each of the three stages (growth, equilibrium, decline) varies, but it appears that usually the stage of equilibrium is longer than either of the other two stages. It is difficult, however, to tell where one stage ends and the other begins, and this is particularly true of the difference between equilibrium and decline.

A few species appear to have increased rapidly in numbers and to have occupied a relatively wide geographic range in a short span of time. This rapid growth was followed by sudden extinction. A good example of this type of distribution is *Carolia floridana*, which spread rapidly over Florida, Georgia, and South Carolina in large numbers but existed for a comparatively short time—approximately 3 million years. This species may have had a narrow ecological tolerance in one or more factors (temperature, type of substrate, etc.), and when the favorable conditions changed slightly, it became extinct.

Species vary somewhat in their speed of dispersion, or their expansion in distribution and in numbers; but the maximum number of individuals of a species and its maximum distribution are attained at about the same time. The maximum distribution of a species will usually be maintained, or nearly so, for a long period during the stage of equilibrium. It is only during the stage of decline that the maximum geographic range of the species also markedly declines. The equilibrium and decline stages also show some variation in amount of time. Length of larval life and other ecological factors may alter the speed of distribution somewhat, but the basic history of distribution seems to be alike for all long-lived species thus far studied.

The direct relation of increase of numbers of individuals of a species to the expansion of geographic range of that species seems to me to place the distribution of organisms on a much sounder biological basis than does Willis' "Age and Area" theory or Rosa's Theory of "Hologenesis." (See Simpson, 1940, p. 140, for a brief review of these two theories.) However, I do agree with Willis that more endemic species are young ones than old or relict ones. Some species never attain a wide geographic distribution because they become extinct before they have lived long enough to expand in numbers and range. It is also true, as Willis states, that many endemic species are young and have

not attained their maximum geographic range.

I do not know whether my idea of the direct relationship of increase of numbers of individuals of a species to its increase in geographic distribution is true of plants, land animals, and fresh-water animals. The applicability must be proved or disproved by the biogeographers who work on these groups of organisms. It is also not known whether the theory applies to genera and groups of higher taxonomic rank.

CONCLUSIONS

From my study of the geologic and geographic history of some late Cenozoic marine pelecypods, I have made the following observations and conclusions.

1. The geographic distribution of a species is controlled mainly by the growth and decline of its populations.

2. As long as a species is increasing in numbers its range of geographic distribution increases.

3. During the period of increase in numbers of individuals, or growth of populations, there is also an increase in the variability of shell morphology. If this is an indication of increasing variability in ecological aptitude to a greater range of environmental conditions, the species continues to spread and occupy additional area.

4. During the period of equilibrium there are minor shifts in geographic distribution due to fluctuations in numbers of individuals. These fluctuations are often caused by changes in the environment, particularly at the margins of the geographic range of a species. However, the distribution of the species remains approximately at the maximum which was reached at the end of the stage of growth or increase of numbers of individuals.

5. During the period of decline in numbers, the geographic range usually becomes discontinuous. Later the species is confined to one or two small areas before it becomes extinct.

MANUSCRIPT RECEIVED NOV. 9, 1952

REFERENCES

ALLEE, W. C., et al., 1949, Principles of animal ecology: 837 pp., 263 text figs., W. B. Saunders Co., Philadelphia.

NICOL, D., 1953a, Systematic position of the pelecypod *Euloxa:* Jour. Paleontology, vol. 27, pp. 56–61, figs. 1–8.

——, 1953b, A study of the polymorphic species *Glycymeris americana:* Jour. Paleontology, vol. 27, pp. 451–455, figs. 1–7.

——, 1953c, Period of existence of some late Cenozoic pelecypods: Jour. Paleontology, vol. 27, pp. 706–707.

SIMPSON, G. G., 1940, Mammals and land bridges: Jour. Washington Acad. Sci., vol. 30, pp. 137–163, 6 text figs.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 26–31, 2 TEXT FIGS., JANUARY 1954

NOTES ON MAMMALS FROM THE UPPER CRETACEOUS LANCE FORMATION OF WYOMING

ALBERT E. WOOD AND JOHN B. S. ORMSBEE
Biology Laboratories, Amherst College

ABSTRACT—A small collection of Cretaceous mammal teeth is described. Multituberculates are represented by 12 specimens of *Meniscoëssus* and 18 of *Cimolomys*. Variants from the patterns previously described are discussed and figured. A peculiar tooth is described and compared with various dinosaurs and with the Paleocene multituberculate genus *Microcosmodon*. While it differs from both, it seems more like the latter. A dinosaur tooth appears to show tooth marks, indicating gnawing by a multituberculate. Marsupial teeth of four types are present. Teeth referred to *Delphodon* and *Pediomys* are unusually small for those genera, and may represent undescribed forms. Insectivore teeth are referred to *Gypsonictops* and *Euangelistes*. The latter differ in size and pattern from previously described specimens.

INTRODUCTION

IN 1948, a field party from Amherst College, led by the senior author, made a small collection of mammals from a blowout on the Altman property, on the Lance Creek-Crazy Woman Creek divide, east of the Lance Creek-Hampshire road, 17.3 miles by road north of Lance Creek, Wyoming. This is the general area where Hatcher made the original collections of Lance mammals (Marsh, 1889a, p. 82) and where a considerable number of collections have since been made. The senior author, together with H. E. and F. D. Wood and others have made several collections of typical Lance mammals from this blowout over a period of some years. In 1948, in a two-day period, 45 mammal teeth were collected, almost all from ant hills in the classic manner (Lull, 1915). All specimens are isolated teeth or tooth fragments.

Most of the specimens are readily identified as belonging to known members of the Lance fauna. One, however, seems to be distinct from all previously described forms, although the material does not permit its certain identification, even as a mammal, much less warrant giving a name. In addition, several specimens of previously described forms give further information of tooth structure or variation in tooth structure that deserve to be put on record as an addition to our rather slender knowledge of the structure of the Upper Cretaceous mammals.

This study was assisted by a grant from the Marsh Fund of the National Academy of Sciences.

SYSTEMATIC DESCRIPTIONS

Order MULTITUBERCULATA
Family PTILODONTIDAE
Genus MENISCOËSSUS Cope, 1882
MENISCOËSSUS ROBUSTUS (Marsh), 1889a
Figures 1A-C

There are a dozen specimens of this species in the Amherst collections. These are generally rather uniform, but show some minor variations.

In Amherst 10401, the buccal half of LM_1, the pattern agrees with that described by Simpson (1929a, pp. 104–105). The anterior of the four comma-shaped cusps has the shortest tail. An elevated ridge, suggestive of a cingulum, runs along the rear end of the tooth. It is somewhat irregular, with what would seem to be secondary outgrowths (fig. 1A). This posterior ridge is only slightly separated from the posterior comma-shaped ridge at its buccal end, but is completely separated at the lingual end by a deep groove. The antero-internal faces of each cusp are marked by irregular vertical ridges. Am. 10402, 10420, and 10439 are identical to this tooth in all essentials of the pattern, but vary in the closeness of the connection between the posterior cingulum and the two ends of the fourth cusp. The buccal valley may be fairly deep, or there may be no visible valley at all. There is always a prominent valley separating the lingual end of the fourth cusp from the cingulum, but it varies in its depth.

Am. 10419 is the postero-external corner of LM_2, almost completely unworn. The vertical ridges in the central valley are limited to clearly defined striations along

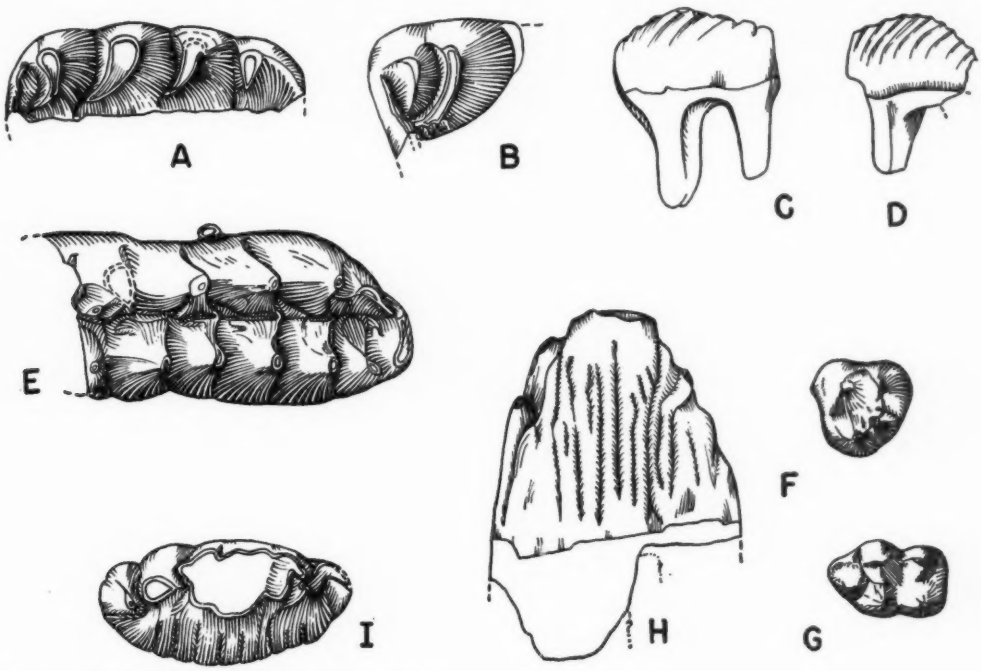


FIG. 1—Multituberculate teeth, mostly ×5.14
A. *Meniscoëssus robustus*, Am. 10401, buccal half of LM_1, anterior end to the right
B. *M. robustus*, Am. 10419, postero-external corner, LM_2, anterior end to the right
C. *M.* cf. *robustus*, Am. 10426, RP_4
D. *Cimolomys gracilis*, Am. 10408, RP_4
E. *C. gracilis*, Am. 10413, LM_1, ×10.28
F. *C. gracilis*, Am. 10436, RP^1
G. *C. gracilis*, Am. 10404, P^3
H. Tooth resembling *Microcosmodon*, Am. 10448, cf. RP_4, ×10.28, lateral view
I. Same, crown view, ×10.28

the lingual end of the crests. The cingular crest is barely separable, either buccally or lingually, from the fourth ridge, and is equally close, lingually, to the third one (fig. 1B). Thus the fourth ridge is much smaller and more curved than in M_1, and the third crest is longer and extends much farther to the rear. The wear surfaces of the cusps are of uniform width, rather than being comma-shaped, as in M_1.

An isolated RP_4 (Am. 10426) is tentatively referred here. It fits within the limits of *Meniscoëssus* in that there are nine serrations along the crown. However, it is 4.1 mm. long, which is only about two-thirds the normal length in Lance members of this genus (fig. 1C). It probably does not fit within the limits of *M. robustus*. There are no accessory roots on this specimen (Simpson, 1936, p. 3) but there are irregularities on both roots which may be the initial stages in the formation of such variants. There is an overhanging ridge along the lingual sides of the roots, which in particular suggests the beginnings of such accessory rootlets (fig. 1C).

Genus CIMOLOMYS Marsh, 1889
CIMOLOMYS GRACILIS Marsh, 1889a
Figures 1 D-G

This is by far the most abundant mammal in the Amherst collection, being represented by 18 isolated teeth.

The lower shearing P_4 is only slightly smaller than that described above for *Meniscoëssus*, but differs in showing very clearly ten serrations along the crest (fig. 1 D). Since the posterior end of the tooth is

broken, it is possible, if not probable, that more were originally present. This number is a characteristic feature of *Cimolomys*. The anterior cavity for P_3 is more pronounced than in the tooth of *Meniscoëssus*.

Three specimens of M_1 are present, of which two seem to have had a cusp formula of 7:6 and one of 7:5. The latter, Am. 10413, shows a fair-sized cuspule arising from the base of the third cusp of the lingual row (fig. 1E). This is presumably of no adaptive or phylogenetic significance, but shows the initial stages from which additions to the tooth pattern could have arisen. A similar accessory basal cuspule is present near the anterior end of the buccal side, blocking one of the valleys between main cusps. In the central part of the tooth, the buccal and lingual cusps are nearly paired, and are connected by curved ridges, crossing the longitudinal valley of the tooth. These ridges are concave forward. Both anteriorly and posteriorly the cusps of the two rows alternate. This tooth is near the maximum size of those referable to *Cimolomys*.

One specimen seems clearly to be P^1 (fig. 1F). There are four cusps, but two of them (the buccal ones?) are closer to each other than are the other pair. Three cusps are united by low crests, only the antero-internal cusp being distinct. This does not seem to be identical with any of the specimens Marsh referred to *Allacodon*, though it is similar to several (Marsh, 1889b, pl. 8, figs. 18–21; 1892, pl. 7, figs. 3–5). A wear facet on the posterior face of the tooth, and the absence of such a facet on the anterior face, shows either that this is P^1 or that there was spacing between the anterior premolars. There are two broad, parallel, transverse roots.

A five-cusped tooth (fig. 1G), agreeing with the type of Marsh's *Allacodon lentis* (Simpson, 1929a, p. 112), is identified as P^3.

Subfamily EUCOSMODONTINAE??
?aff. MICROCOSMODON, gen. et sp. nov. indet.
Figures 1H–I

An isolated tooth, Am. 10448, is apparently quite different from anything previously described from the Lance (figs. 1H–I). The tooth is triangular in side view, with a broad base and more or less equally tapering anterior and posterior sides. The antero-posterior diameter (3.2 mm.) and height of crown (2.9 mm.) are approximately equal. The transverse diameter is much less (1.6 mm.). The upper margin of the crown is surmounted by either six or seven cuspules, the uncertainty being due to wear on the apical cusp or cusps. Although all the cuspules show wear, there is a much larger amount at the apex than elsewhere. One side of the tooth shows a series of shallow grooves, radiating from the notches between the separate cuspules (fig. 1I). The other side shows about 15 narrow, deep striations, which do not seem to have any relationship to the cuspules on the crown (fig. 1H). The roots of the tooth are broken, and it cannot certainly be determined whether there were two roots (as suggested in fig. 1H), or whether there was only one. The side with the narrow striations certainly had no shelf at the base. The other side does not seem to have had one, though there is a possibility that one had been present.

This tooth was compared with a variety of forms, but has not been matched in anything we have seen or have seen described.

Perhaps the closest resemblances are to RP_4 of *Microcosmodon conus* (Jepsen, 1940, pp. 320, 321, and pl. 5, figs. 3 and 3a). There are clear differences between the two, not surprising in view of the time gap between Upper Cretaceous and middle Paleocene. The tooth is approximately twice the size of that in Jepsen's form, and the number of cuspules is larger, there being five in *M. conus*. There is a labial cingulum in *M. conus*, but this area is somewhat broken in the present specimen. No suggestion of the fine striations is seen in *M. conus*.

There are resemblances between this tooth and Marsh's figures of *Oracodon conulus* (Marsh, 1892, pl. 7, fig. 8), but the differences are very obvious, and are even more apparent from Simpson's figures and description (1929a, pp. 105–106 and fig. 42). There therefore does not seem to be much likelihood that this is an upper premolar of a multituberculate.

The tooth shows some resemblances to teeth of ceratopsians (Hatcher, Marsh and Lull, 1907, pp. 43–45 and figs. 42–46), but comparison with ceratopsian teeth and with

the figures and descriptions of them in the Ceratopsia monograph indicates clear differences in pattern, shape and arrangement of the cuspules. In addition, there appear to have been two roots, in an antero-posterior row, in Am. 10448, and the enamel has a coloration and general appearance much more like that of the mammals than of the reptiles in the Lance faunule.

Comparisons have been made with various other dinosaur teeth, also without finding any close correlatives. The teeth of the troödont, *Pachycephalosaurus* (Brown and Schlaikjer, 1943, pl. 40, fig. 1) are quite similar, but have a dozen or more cuspules and are three times the size of the present specimen. Moreover, there is no suggestion of the striations, and there is but a single root. There is a similarity, however, in the absence of a basal shelf in *Pachycephalosaurus*. The teeth of such ankylosaurs as *Stegopelta* and *Palaeoscincus* also show similarities. The number of cuspules is smaller, being eight in *Stegopelta* (Moodie, 1911, p, 261). Here there are strong, divergent roots. But again the teeth are large, being over twice the size of the Amherst tooth, and there is a basal shelf on one side toward which the cuspules converge. Nor are there any of the fine striations. *Palaeoscincus* is even less similar to the specimen shown in fig. 1H–I (Brown, 1908, pp. 190–192, figs. 4–7).

In summary, this tooth is certainly different from everything with which it has been compared, and seems to represent a form not previously reported from the Lance. The cusp pattern and the coloration of the enamel suggest a mammal. While some dinosaur teeth are two-rooted, the presence of two roots (if there were two) suggests that it is a mammal. While there are clear differences from the teeth of any mammal with which comparisons have been made, it most closely resembles *Microcosmodon*, but is certainly generically distinct from that form. Actually the teeth of *Microcosmodon* are more like those of *Stegopelta* and *Pachycephalosaurus* than any of them are to Am. 10448.

MULTITUBERCULATE GNAWING

An isolated ceratopsian tooth (Am. 10345) shows a remarkable groove cut diagonally across the root. In this, there are a series of parallel striae, about 0.15 mm. wide, and running parallel to the direction of the notch. If this were from rocks of Tertiary age, it would be considered to be the work of rodents. Presumably, in the present case, it represents gnawing by a multituberculate. The individual striae are fine, and do not fall into pairs as is usually the case with rodent incisor marks. This probably reflects merely the narrower tips of the incisors in multituberculates, rather than the possibility of the gnawing having been done by an animal with a broken incisor (Hooijer, 1951).

Order MARSUPIALIA
Family DIDELPHIIDAE
Subfamily DIDELPHODONTINAE
ECTOCONODON PETERSONI Osborn, 1898
Figure 2A

Two upper molars are referred to this species. The most striking feature of Am. 10412 is the broad wear surface that extends from the tip of the metacone down into the valley in front of it, and part way up the posterior side of the paracone (fig. 2A). This worn section widens out in the central valley, and has an area greater than the sum of the wear surfaces on the tops of the cusps.

SIMPSON TYPE 8, 1929a
Figure 2B

A lower molar of this type shows a highly worn and partly broken protoconid and metaconid, and a little worn paraconid isolated from the other cusps (Am. 10433, fig. 2B). The talonid is basined, and closed posteriorly by a hypoconulid weakly united with the hypoconid. A small fragment of a basal cingulum is present below the paraconid. A similar cingulum extends across the posterior margin of the tooth, fusing lingually with the hypoconulid.

DELPHODON sp.
Figure 2C

A left lower molar (fig. 2C) is referred to this genus. It is typical in pattern for *Delphodon*, but differs in its extremely small size, being only a shade over 2 mm. long. In this character it agrees with the lower molar Type 5 of Simpson (1929a, p. 133), but differs in having the low trigonid of *Delphodon*. Unless this represents a very

small form of *Delphodon*, it does not seem clear what it could be.

Subfamily PEDIOMYINAE
PEDIOMYS Marsh, 1889a
Figure 2D

A very small tooth, Am. 10447, is referred to this genus, although it is smaller than the limits given by Simpson (1929a, p. 119). The tooth is longer than it is wide, with a rounded metacone and a paracone that grades continuously into the parastyle at the anterior end of the tooth (fig. 2D). The extreme anterior and posterior tips of the tooth are missing, but there was clearly a parastyle at the anterior tip. Probably the absence of the parastyle is due to interdental wear rather than to breakage, since the surface at the end of the tooth is smooth. The conules are small, the metaconule in particular being merely a swelling of the posterior cingulum. The wear surface is continuous from the metacone through the paracone to the parastyle. In the central valley, the worn area expands to extend over half way to the protocone, in the bottom of the basin. Three small styles are present along the anterior half of the buccal margin.

This specimen also shows considerable resemblances to the upper molar of *Synconodon sexcuspis* (Osborn, 1893, pl. 8, fig. c) with which it agrees in its small size. It differs from this figure, however, in the presence of styles A, B, and C (Simpson, 1929a, p. 119).

Order INSECTIVORA
GYPSONICTOPS HYPOCONUS Simpson, 1927
Figure 2E

Am. 10438 (fig. 2E) is the lingual portion of an LM^2 of this form. It agrees well with the common type of this tooth as figured by Simpson (1951, fig. 2a). The wear surface of the protocone extends buccad as far as this specimen is preserved, probably including the conules in its area. The small enamel lakes preserved at the buccal margin of the specimen presumably are pits between the conules and the buccal cusps. Both anterior and posterior cingula are well developed.

EUANGELISTES PETERSONI Simpson, 1929b
Figures 2F–G

Two isolated teeth are referable to this species. Am. 10442 (fig. 2F) is apparently

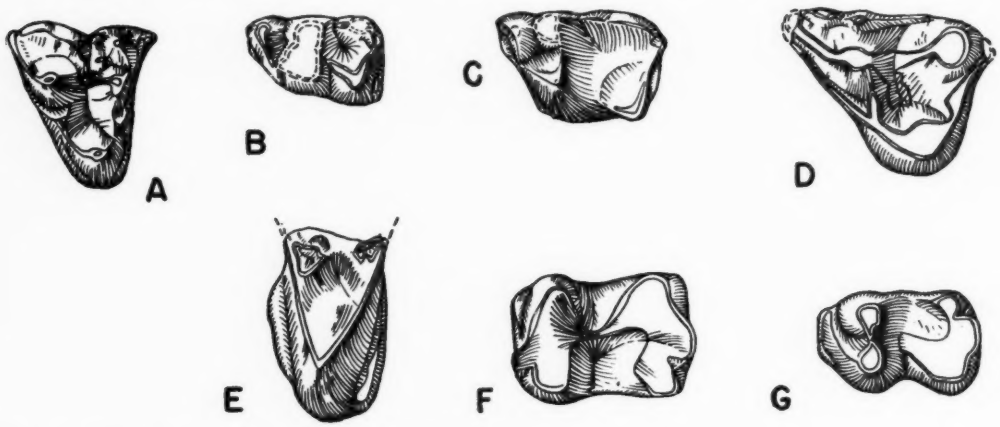


FIG. 2—Marsupial and insectivore teeth, mostly ×10.65
A. *Ectoconodon petersoni*, Am. 10412, left upper molar, ×5.33
B. Didelphodontine, Type 8, Am. 10433, left lower molar, ×5.33
C. *Delphodon* sp., Am. 10443, left lower molar
D. *Pediomys* sp., Am. 10447, LM^4
E. *Gypsonictops hypoconus*, Am. 10438, LM^2
F. *Euangelistes petersoni*, Am. 10442, RM_1
G. *E. petersoni*, Am. 10450, LP_4

M_1, since the trigonid and talonid are essentially of equal diameters (1.53 mm. and 1.49 mm., respectively). The paraconid is reduced but is still fairly large and is closely united with the metaconid in the stage of wear represented by this specimen. The wear surface of the paraconid extends down onto the anterior face of the tooth, so that its anterior portion looks as though it might have worn against P_4. There is an anterior cingulum on the buccal half of the tooth, and no trace of a posterior cingulum.

The other tooth (Am. 10450) was at first identified as LM_1 on the basis of the equal diameters of the trigonid and talonid. Further analysis suggested that it represents P_4, because of the small size (width of trigonid and talonid each 1.27 mm.). On the other hand, it differs from that tooth as described by Simpson (1951, p. 11) in that there is clearly a crest running linguad from the anterior side of the protoconid, suggesting a vestigal or incipient protolophid (fig. 2G). This crest drops rapidly from the protoconid to the antero-internal corner of the tooth where it blends into the anterior cingulum, which turns abruptly back toward the buccal side of the tooth. There is no trace of a distinct paraconid, although wear might suggest one. There is a short posterior cingulum on this tooth, but it is hidden in crown view by the overhang of the hypoconulid.

The second tooth suggests two possibilities:—this may represent M_1 of a smaller species of *Euangelistes* than *E. petersoni*, or it may represent an unusually molariform premolar: If the latter is the correct interpretation, there must be a considerable range of variation in P_4 of this species.

MANUSCRIPT RECEIVED MARCH 27, 1953

REFERENCES

BROWN, B., 1908, The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous: Bull. Amer. Mus. Nat. Hist., vol. 24: 187–201.

——, and SCHLAIKJER, E.M., 1943. A study of the Troödont dinosaurs with the description of a new genus and four new species: Bull. Amer. Mus. Nat. Hist., vol. 82: 121–149.

COPE, E. D., 1882, Mammalia in the Laramie formation: Amer. Nat., vol. 16: 830–831.

HATCHER, J. B., MARSH, O. C., and LULL, R. S., 1907, The Ceratopsia: U. S. Geol. Survey Mon. 49, 300 pp.

HOOIJER, D. A., 1951, The supposed evidence of early man in the middle Pleistocene of southwest China: Southwest. Jour. Archaeol., vol. 7: 77–81.

JEPSEN, G. L., 1940, Paleocene faunas of the Polecat Bench formation, Park County, Wyoming. Part 1: Proc. Amer. Phil. Soc., vol. 83: 217–340.

LULL, R. S., 1915, Ant-hill fossils: Popular Sci. Monthly, pp. 236–243.

MARSH, O. C., 1889a, Discovery of Cretaceous Mammalia: Am. Jour. Sci., ser. 3, vol. 38: 81–92.

——, 1889b, Discovery of Cretaceous Mammalia. Part II: Am. Jour. Sci., ser. 3, vol. 38: 177–180.

——, 1892, Discovery of Cretaceous Mammalia Part III: Am. Jour. Sci., ser. 3, vol. 38: 249–262.

MOODIE, R. L., 1911, An armored dinosaur from the Upper Cretaceous of Wyoming: Kans. Univ. Sci. Bull. 5: 257–273.

OSBORN, H. F., 1893, Fossil mammals of the Upper Cretaceous beds: Bull. Amer. Mus. Nat. Hist., vol. 5: 311–330.

——, 1898, Evolution of the Amblypoda. Part I. Taligrada and Pantodonta: Bull. Amer. Mus. Nat. Hist., vol. 10: 169–218.

SIMPSON, G. G., 1927, Mammalian fauna of the Hell Creek formation of Montana: Amer. Mus. Novitates, no. 267: 1–7.

——, 1929a, American Mesozoic Mammalia: Mem. Peabody Mus. Yale Univ., 3, pp. i–xv, 1–235.

——, 1929b, Some Cretaceous mammals from the Lance formation: Ann. Carnegie Mus., vol. 19: 107–113.

——, 1936, A specimen of the Upper Cretaceous multituberculate *Meniscoëssus*: Amer. Mus. Novitates, no. 825: 1–4.

——, 1951, American Cretaceous insectivores: Amer. Mus. Novitates, no. 1541: 1–19.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 32–42, PLS. 3–6, JANUARY 1954

PRIMARAUCARIA, A NEW ARAUCARIAN GENUS FROM THE VIRGINIA TRIASSIC

WILHELM BOCK
Academy of Natural Sciences, Philadelphia

ABSTRACT—The new genus and species *Primaraucaria wielandi* from the Upper Triassic of Richmond, Virginia, seems to be the earliest known representative of the family Araucariaceae. The female strobilus shows close relationship to living forms, but the male inflorescence is much more primitive, displaying paired sporangia, covered by and partially attached to a protective bract. Close to the lower part of the female and particularly of the male cone, the foliage is greatly modified, forming a "pericone," an aggregate of closely set whorls of enlarged bracts, which appear to protect the cone. The spirally arranged leaves of the fertile shoots appear to be of two forms, one restricted to the male, the other to the female, or both to the same shoot, a condition called "sexfoliation." The foliage of some branches of *Primaraucaria* is arranged in two spirals around the stem, the leaves of one spiral being different in form from those of the other.

INTRODUCTION

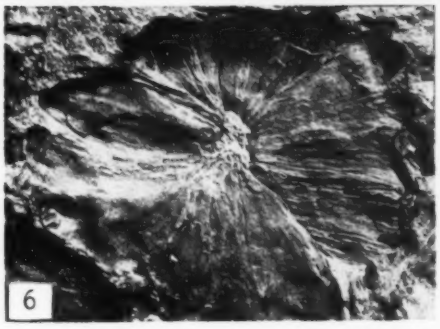
IN THE course of completing the paleobiological records of the eastern American Triassic, systematic exploration of the fossil beds in the Richmond coal basin, Virginia, was begun about 5 years ago. All known coal mines and dumps were examined, but with quite discouraging results. Then, shortly before the search was abandoned, the scattered rocks at a bridge abutment, just previously dumped, were given a casual inspection. In a short time, this unpromising place yielded a dozen different species of plant fossils, including a coniferous cone. The original source was traced, with the help of a local boy, to a coal mine dump at Clover Hill, Chesterfield County, where highway department trucks were in the process of spreading the Triassic deposits over many other formations. Little could be done about this, but the gradual removal of the rocks helped to uncover from the intermingled strata fossiliferous layers that yielded excellent specimens of portions of the Upper Triassic flora similar to those assembled by W. M. Fontaine (1883).

A number of new species were likewise unearthed. These will be described in a series of articles. While the dump has now been largely removed and its paleontological usefulness exhausted, several thousands of plant fossils and imprints, together with fish remains and estherids, have been recovered for future studies. It is possible that other mine dumps may hide similar fossil treasures, although none have yet been found. The Midlothian coal mines, located in the same formation as those at Clover Hill, are promising, and because of their wide extent hold out some hope for more fossil plants.

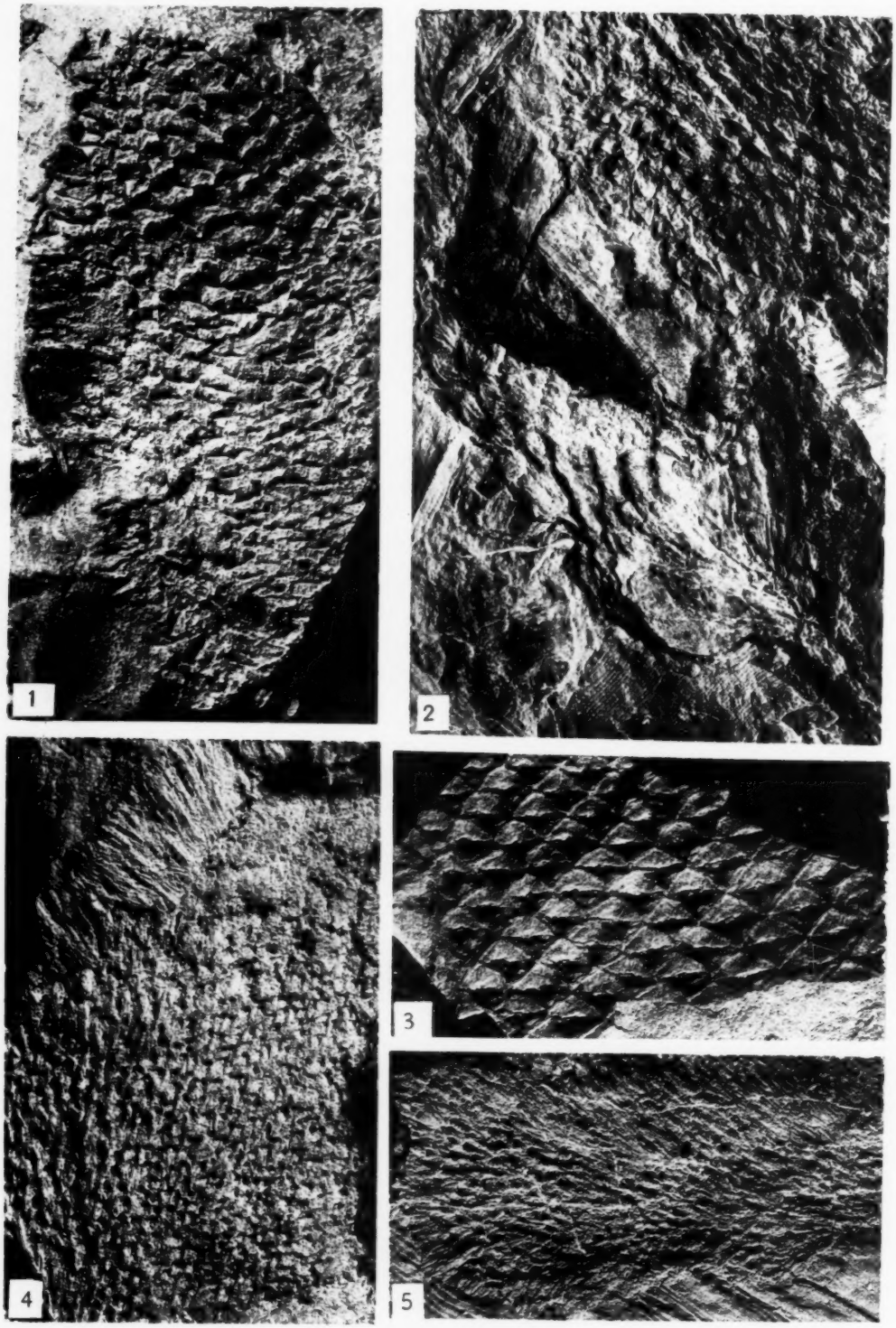
The old Clover Hill mines were located in the so-called "Virginia Coal Measures," which, overlain by the Vinita sandstone, form the eastern border of the Richmond basin. They represent some of the oldest deposits of this section. Since the layers dip in a western direction, and as the removal of the overburden of the mine may have followed any direction, the accumulated rocks, dumped in an arbitrary fashion, do not disclose their sequence of deposition.

EXPLANATION OF PLATE 3

FIG. *1*—Foliation on branch of last order of *Primaraucaria wielandi* displaying spirals of imbricate leaves. ×2.
2—Continuation of branch shown in fig. *1*, ×2.
3—Tip of ultimate branch shown in fig. *1*, ×2.
4—Impression of separate branch of the same species showing leaf wrinkles.
5—Proliferous growth from male pericone in a foliated branch. ×1.
6—Detached male pericone. ×2.



Bock, Triassic *Primaraucaria*



Bock, Triassic *Primaraucaria*

However, a reasonably close picture of their consecutive order can be visualized from the nature of the rocks and the fossils that they contain.

The youngest type of rock encountered is a brick-red, unstratified sandstone, disclosing scarcely any fossils. A more red-yellow sandstone contains numerous, macerated, silicified wood particles, many seeds and some *Equisetum* remains. The most productive layer was a much finer grained, rather soft, well laminated reddish-brown to tan-colored shale. This layer apparently preserved the majority of all plants, which flourished at that location in Triassic times. A carbonaceous gray to black shale, which contained fewer plants, but more woody debris, is believed to have been deposited closest to the coal-bearing strata, since the plant remains of this shale layer are largely carbonized, in contrast with the tan shale layers, which contain mostly imprints. Conglomerates were not observed in these deposits.

As to why the tan-colored shale deposits were unable to preserve the plant matter, it should be mentioned that leaves, particularly those belonging to the genus *Taeniopteris*, deposited in thick accumulations and doubtless under water, appear to have fallen closely one over the other. Microscopic examination shows that all carbonaceous matter was removed, probably by oxidation due to the high ferric oxide content of the deposits. The remaining crevices of the plants have been penetrated by very fine sediment of the same lithological nature as the surrounding rock. The surface impressions are, therefore, in many cases so well preserved that microscopic details are clearly distinguishable.

The conifer to be described in this paper comprises specimens primarily preserved in the tan roof shales, but several other remains of it, including stem portions with leaves, are from the grayish-black shale, in which they became carbonized. Numerous, morphologically different parts of this tree were secured, of which the most notable are some 20 male and female strobili, including several immature female ones. The cones, particularly the male strobili, are surrounded at the base with closely set whorls of enlarged leaves or bracts, which arrangement is called a "pericone." Foliated branchlets were in some layers quite abundant. The spirally arranged, scaly leaves of the fertile shoots appear to be of two forms, one restricted to the male, the other to the female shoots. The foliage of some leafy branches is often arranged in two spirals around the stem, the leaves of one spiral being different in form from those of the other spiral. For this condition the term "sexfoliation" is here introduced.

Only in two specimens could a direct connection be recognized between the foliage and the cones. In one specimen recognition was based on proliferous growth. However, the many isolated parts of this tree were always found associated closely with other portions of the same species, so that their mutual relationship appears to be well founded.

SYSTEMATIC PART

CONIFERALES

Family ARAUCARIACEAE Strassburger 1872

Genus PRIMARAUCARIA Bock, n. gen.

Generic description.—Leaves triangular, scale-like, thick, wrinkled or smooth, compressed, overlapping rhomboidally, spirally arranged on a rigid stem; female cone ovoid to ellipsoid with one-seeded, elongated cone scales terminating in an apophysis of rhomboidal shape with a central umbo and median lip; immature female inflorescence elongate ovoid with linear, oblong scales, arranged on a thick axis; male cone cylindrical to funnel-shaped, surrounded at base

---

EXPLANATION OF PLATE 4

FIG. *1*—Type of male cone of *Primaraucaria wielandi*. ×1.
2—Female and male cone with obscure foliage. ×1.
3—Section of female cone with distinct apophysis. ×2.
4—Female inflorescence showing bract scales. ×5.
5—Female inflorescence, slightly older than the one of fig. *4*.

by a pericone. Genotype: *Primaraucaria wielandi*, the only species.

PRIMARAUCARIA WIELANDI Bock, n. sp.
Plates 3–6

Foliaceous branches.—Flattened branches of last order fully foliated to a length of 40 cm., originally cylindrical, straight, stiff, extended, sparsely sub-branched, about 10–12 mm. in diameter, having a blunt, rounded tip (pl. 3, fig. 3). Stem proper of small diameter, about 2–3 mm., covered with closely arranged, overlapping, appressed scale leaves lying nearly parallel with the stem in two spiral series at 35 to 40 degree angles, about seven leaves to a full turn.

Foliage.—Leaves scale-like, triangular to ovate, bifacial, concave adaxially, thick at base, thinning out toward apex, 8–10 mm. long, 5–6 mm. wide; usually having surface broadly curved, striated, some with a vague keel and indentation, longitudinally; apex roundish to moderately pointed; apical portion showing two to three transverse wrinkles, being prominent on younger, absent in older, foliage; lower portion of leaf contracting to a short, curved base, attached at nearly a right angle to branch axis, forming a lens-shaped (about 1 mm. wide) contact point; epidermal striae varying from 8–12, covering outside surface of leaf; epidermal pattern disclosing parallel chains of rectangular cells, about 0.03 mm. wide, with rows of obscure widely spaced stomata. Sexfoliation expressed by two distinct leaf types, each arranged on a spiral, one type being thin, smooth and short, the other longer, thick walled and coarse.

Female strobili.—Macrosporangiate strobili ovoid to ellipsoid, varying in length and shape; average length 8.5 cm.; maximum diameter 4 cm.; other fragments indicating up to double this size; cones mostly solid, loosening at maturity, but not disintegrating; scales arranged in rows of 30 to 40, of about 8–12 spirals, surrounded at the base by three to four turns of slender, acuminate, imbricate leaf scales, forming a modest pericone; individual macrosporophyll triangular, sector-like, terminated by a pronounced apophysis; length varying from 10–15 mm., width 3–5 mm.; upper side of scale slightly concave, disclosing about six thin veins and the impression of a single oval seed, covering about half of the lower portion of the scale; lower side convex, keeled, finely striated; apical cross wrinkle indicating fused seed and bract scale, forming a compound apophysis; width varying from 4–8 mm. and height 3–4 mm., having rhomboidal shape, being divided by a median, horizontal lip, centered by a more or less protruding small umbo; several lines or grooves radiating from umbo of apophysis, two forming an acute angle of 70–80 degrees in upper portion; coarse dermal surface of minute granular design typical of apophysis.

Female inflorescence.—Young, female strobili (pl. 4, figs. 3, 4) nearly ellipsoid with slender, flexible apex, about 25 mm. high, 16 mm. wide, having closely but somewhat loosely, spirally arranged scales, attached to a conical, thick, flexible stem 5–7 mm. wide; scales single, linear, flat, 5 mm. long, 0.3 mm. wide, thickening toward apex to an acuminate, slightly falcate head; surface of scale divided in about 12 rows of rectangular cells, 0.03 mm. wide, three to four layers thick, marked by six fine, epidermal ridges; base of scale flat, slightly thickened, sessile upon stem surface; stem axis thick, considerably reduced at both ends, consisting of peripheral vascular strands, rows of tracheid cells and pith cells in the center.

Male strobili.—Candelabra-like, based on three to four rows of closely-set whorls of enlarged, longitudinal, spreading leaves, gradually replaced upwards by smaller and more roundish scales, arranged in eight spirals of about 50–60 scales, closely appressed to a thick, subcylindrical stem; average length of strobili 35 mm. Scales emerging from the leaves of the pericone, strongly curved, roundish, slightly longer than broad, overlapping, some with clasping tips; lower portion of scale contracting at the base to a short bracket, curved toward cone axis and attached in small notch of integument surrounding stem. Scales cover a pair of symmetrically arranged sporophylls, attached by a small, short bracket to stem integument and basal portion of scale; openings in the integument indicate different vascular supply channels; sporangia obscure elongated, oval, flat bags imbedded in curved interior portion of scale.

Comparison with fossilized araucarian remains.—There are numerous araucaria-like trees reported as far back as the Upper Carboniferous age. The older ones, up to the Triassic, have been regrouped by Florin (1944) in the genera *Lebachia* and *Ernestiodendron*. Younger ones have been united in the broad collective genus *Araucarites*, generally representing separate morphological portions of little conclusive identification value. Some actual araucarian resemblance is shown by the Permian species *Araucarites delafondi* Zeiller and the cone *Araucarites sphaerocarpa* Carruthers of the English Oölite. A true araucarian cone is *Pararaucaria patagonica* Wieland from the Cretaceous of Argentina. From the later Mesozoic on, araucarian remains with characteristics resembling those of the Recent species, became more frequent, but a really complete morphological account of a single species has been wanting.

In Triassic rocks araucaria-like cones, similar in structure to those of *Araucarites sphaerocarpa*, and separate foliage, were found in the Lockatong formation of the Newark Basin (early middle Keuper) at Gwynedd. Some are reported from the Triassic of more southern regions, Thus, Fontaine (1883, p. 85, pl. 47, figs. 4, 5) described *Zamiostrobus virginiensis*, which represents an araucarian cone closely related to *Primaraucaria*. The same author recognized *Zamiostrobus* Emmons (1857, p. 123) as an araucarian cone, Emmons having believed it to be a cycadean trunk. A pericone impression with scale-like sectors was described by Emmons as *Lepacyclothes circularis*. Fontaine (idem, p. 119) identified it as an araucarian type of cone and changed the name to *Araucarites carolinensis* (although it should be *A. circularis*). The impression doubtless represents a portion of a detached pericone of an araucaria-like strobilus similar to that of *Primaraucaria*. The cone apparently becomes easily detached from the pericone. Daugherty (1941, pl. 15, fig. 1, 2, p. 81) shows the impression of flattened-out whorls of leaves or scales, resembling the pericone of an araucarian male strobilus. There are about eight to ten compressed whorls with pronounced veins, which are comparable to the flower of *Williamsonia*. The inflorescence of this genus has been so far unknown in the middle Keuper, to which these Triassic horizons of Arizona and Virginia belong. However, there are several species of *Weltrichia* Braun known from the Rhaetic, the flower of which forms an incomplete cup consisting of a whorl of about 20 linear sectors having separate lanceolate lobes with a midrib. While Emmons' and Daugherty's plants bear a superficial resemblance to the *Weltrichia* flower, their actual nature seems to be closer to the pericone of an *Araucaria*.

Another apparently female strobilus is reported from similar Triassic strata near York, Pennsylvania, as *Araucarites yorkensis* Fontaine (Ward 1898–99, pl. 34, fig. 5, p. 311). It appears that araucaria-like trees were well represented throughout the eastern and western Triassic. Kendall (1949, pp. 151–161) describes a Jurassic member of the Araucariaceae as *Araucarites phillipsi* Carruthers, with female scales having a ligule(?), and a male cone of *Brachyphyllum mamillare*, the microsporophylls of which have a hypopeltate shape, being arranged in an imbricate manner. Both species appear to be of araucarian affinity.

Locality.—Abandoned mine dump at Clover Hill, near Winterpock, Chesterfield County, Virginia. Virginia coal measures, below the Vinita sandstone. Upper Triassic, correlated with the upper part of the European Keuper (Knollenmergel).

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype no. B-200201. Paratypes nos. B200202-216. Paratype, female cone, Peabody Museum, New Haven, Connecticut.

MORPHOLOGICAL AND PHYLOGENETICAL COMPARISONS

Before a close comparison of the fertile and foliage portions of *Primaraucaria* and its relationship to other conifers, can be attempted, some previous findings in this field should be cited.

The male strobilus.—Florin (1940–45, 50) discussed in an elaborate treatment of the fossil and recent stachyosperms the phylogenetic succession of the conifers, beginning with the Cordaites and coordinating the Paleozoic and older Mesozoic conifers in a more or less natural sequence, including an

almost inexhaustible source of morphological details. He sees as the ultimate origin of the coniferous female flower a fertile dwarf shoot and its bract, the shoot bearing spirally arranged sterile and fertile scales. He does not consider the seed scale to be derived from a foliated element. The Cordaitales are grouped by him in the *Cordaianthus pseudofluitans* type, and the somewhat younger one *Cordaianthus zeilleri*. The contemporaneous Paleozoic conifers are united in his new genus *Lebachia* and *Ernestiodendron*, eliminating the well-known group *Walchia* as of full generic rank. The Mesozoic conifers, of which the most important are the Lower Triassic genus *Voltzia* and the Upper Triassic *Schizolepis*, have been also discussed by Florin (1944) in detail. He states that these two genera indicate a fusion of the fertile and sterile scales as far back as the older Mesozoic. The female organs of the genus *Schizolepis* consist of three sterile scales, with which a triple megasporophyll is partially fused along the proximal portion.

Wilde and Eames (1948), who described the ovule and seed unit of *Araucaria bidwilli*, show a reconstructed side view of *Schizolepis* (fig. 19) with the four different elements involved, the subtending bract, the sterile scale fused with the fertile one and the apical free, pendulous ovule. The authors conclude from the distribution of the vascular supply system in *Araucaria bidwilli*, that the single ovule of *Araucaria* is a survivor of three, thus indicating relationship to the Upper Triassic *Schizolepis*. Wilde and Eames (idem, p. 314) also recorded different growth stages of the female organ not long before pollination (fig. 2). In this phase the length of the seed scale is about half that of the bract scale and free from the latter at the distal half. At fertilization, a year later, the fertile scale is nearly as long as the bract. At full maturity the size of the ovule is about three-quarters that of the seed scale, the latter only free at the apical tip from the bract scale. No sterile scale is pointed out. According to Hirmer (in Florin, 1944, p. 514) the apical tip represents the sterile element. The seed scale unit (Florin's seed scale complex) apparently forms with the bract scale a pronounced apical apophysis as in *Primaraucaria*.

The closed female strobilus of Primaraucaria.—Comparing the female organs of *Primaraucaria* with those of *Schizolepis* little if any resemblance is found to exist between the two genera, in spite of their similar age (middle Keuper.) The complete cone of this new genus is close to that of the modern *Araucaria brasiliensis* and *A. angustifolia*. The characteristic conical shape of the female strobilus, the nature of the scale spirals, the triangular form of the scale units, the single seed and the typical apophysis, the scale leaves preceding the scales, forming a modest pericone, all clearly betray a close araucarian relationship between these Recent species and *Primaraucaria*. The tightly set apophyses form a complete "super ovule," within which the seeds grew fully protected. This may be the earliest record of a coniferous, weatherproof and fully closed cone structure.

The apophysis.—Two halves form the primaraucarian apophysis, the upper being provided by the seed scale unit and the lower by the bract scale. The median lip is apparently the contact line of these scales. In some of the cones, the upper half of the apophysis is less developed and does not protrude, giving the apophysis a triangular shape. In others, they are so tightly compressed, lengthwise, that they form occasionally a hexagonal pattern, resembling that of some cycads. The construction of the apophysis by two different scale elements, a foliar and a reproductive one, is in complete contrast to that of the pine family, where the bract scale has no part in shaping the distal portion of the seed unit.

The combined scale unit.—While the cone scales of present araucarians are caducous, those of *Primaraucaria* seem to detach only very slowly. As most of the cones which have been found differ greatly in size, one suspects that they may represent different stages of growth. Only two partially carbonized cones were found with a few detached scales. The general shape of the latter, which also varies in the different portions of the cone, is close to that of *Araucaria bidwilli*, representing a more or less variable sector-like form with a tip terminating the apophysis. The apical portion is curved slightly upwards, while the median portion shows a broad indentation of shallow oval shape, indicating the position of a

single seed. Curiously, the latter was never found. Seed and bract scale are not distinguishable on the surface, as they are apparently fully fused. Only in some scales is an apical cross crack visible, which may terminate the seed scale. As the upper portion of the apophysis is believed to be formed by the seed scale unit, this element, when mature, probably covered the whole surface of the bract scale. No intermediate sterile scale was observable.

The young female inflorescence.—The female catkin, of which several were found (pl. 4, figs. 4, 5), could be recognized as primaraucarian by the surface features of the cone, scale shape (the lower ones resembling closely those of mature cones), spiral angle, number of scales and typical scale leaves in the stem transition zone. The straight linear shape of the immature scales, having a small apical falcate head, is characteristic only of the bract scales at that particular age. On the surface of some scales there is a thickened portion near the base, which suggests the beginning of the seed scale unit. Little comparative material in Recent species of this early stage is available. The apical falcate head of the early bract scale is quite thick, compared with the remainder, and it is believed that it forms part of the apophysis later on. It is the only part which protrudes from the female inflorescence, and it probably plays a role in the reception of the pollen grains during the pollination period. Burlingame (1913, figs. 10, 11) noted that the pollen grains of *Araucaria brasiliensis* fall on the apical end of the bract scale. From there the pollen tubes extend to the interior toward the base of the ovule. Some minute lens-like grains are visible on the apical surface of a few premature scales of *Primaraucaria* suggesting a similar condition.

The male strobilus.—Before any intelligent discussion of the male strobilus can be undertaken, the excellent reproductions of fossil coniferous male "flowers" by Florin (1944) should be consulted. This author concludes that the earlier conifers such as *Lebachia hypnoides* or the single strobilus *Walchianthus* bore microsporophylls or microsporangial scales, which were spirally arranged around an axis. They consisted of a stalk, terminated by a hypopeltate, leaf-like, acuminate bracket, from the lower side of which sporangia extended toward the axis of the cone. From Florin's pictures, showing a cross-section of a male cone, it can be concluded that the strobilus had an imbricate appearance with sporophylls similar to those of some Recent species such as *Araucaria muelleri.*

The microsporophyll.—Pilger (in Engler and Prantl, 1926) discussed broadly the Recent coniferous male flower, which he compares with a foliage leaf, terminating in a shield-like growth, for which he visualizes the structure of the so-called hypopeltate scale (fig. 112). According to Pilger, the pollen sacs were basally located on the lower side of the leaves, similar to those of the cycads. The microsporangia of the largest number of living conifers appear to be attached to the lower portion of the shield, yet the different variations and intermediate forms suggest that there is no conclusive proof for suspecting the origin of the sporangia on the lower side instead of the upper side of the sporophyll scale. The young male inflorescence of *Pinus nigra* has basal leaves of a heart-shaped form, the lamina of which becomes replaced along the margins by two longitudinal pollen sacs. The upper terminals of the sacs form with the upwardly bent remainder of the lamina a chlorophyll-bearing protective shield. Ontogenetic data as to male strobili on Recent conifers are meager. Burlingame (1913, p. 102) gives some details about the microsporophyll of the living *Araucaria brasiliensis*, citing several developmental stages. The first sign is a somewhat mushroom-like growth deriving from meristematic cells, forming a kind of peltate shield, from the lower portion of which the sporangia emerge. The distal shields develop in a tightly set, tile-like, cone surface. This structure appears to be of an advanced type.

The more primitive araucarians seem to be represented by another group headed by *Araucaria muelleri* Carriere, which develops a pronounced pericone and overlapping sporophyll scales. The latter are not peltate but somewhat heart-shaped with pollen sacs occupying a position lateral to the stalk. This shape is similar to that of *Lebachia hypnoides* Florin (1944, p. 436). Two types of male cone mechanism can be, therefore, distinguished. The imbricated type which is not perfectly tight and the

tile-like form, which is practically a weather-proof enclosure. Most Recent conifers have a reduced cone axis and a lengthened stalk, while the fossil species of the Triassic still display a relatively thick, expanded stalk.

The character of the pericone.—The pericone, consisting of whorls of long, modified, closely-set leaves around the base of the strobilus, is a character typical of *Primaraucaria* and of, more or less, the living *Araucaria muelleri*. It can be argued that the pericone is properly an element of the strobilus. However, this cluster of leaves is certainly a transition component, which appears always in combination with a reproductive organ, unless the cone was broken off (pl. 3, fig. 6). The thick and enlarged pericone leaves are believed to be adaptive for food and water storage and possibly for protection.

Microsporophyll scales of Primaraucaria. —These scales are curved, roundish, thick shells arranged nearly parallel to the cone stem. The scales contract at the base to a short bracket which is attached more or less vertically to the integument of the stem. A median indentation on the outer and inside surface, with addition to two clasping tips (pl. 5, fig. 1), indicates a two-sectional symmetrical origin. The scale covers a pair of sporophylls, of which an immature one with a short curved bracket attached to the cone stem, may be seen on plate 5, figs. 1c and 2. The protective scale has been broken off. What appears to be firmly established by the disclosure of the primaraucarian male cone is the fact that the sporangia are located on the inside (upper side) of the bract scale, attached to the basal portion, and not below the scale.

To find a parallel development, *Austrotaxus spicata* Compton may be cited. Plate 6, fig. 13 (from Saxton, 1934, fig. 21) shows the cross-section of the male cone of this species with the sporangia attached to the axil of the bract scale by a short stalk, all elements being supplied by separate vascular strands, which are combined to one when entering the thick cone axis. The similarity of this microsporophyll structure to that of *Primaraucaria* is striking, although the female organs are different. Florin (1945, p. 657) explains the extraordinary conditions of this Recent microsporophyll structure as a "flower, which is extremely reduced." Actually, it seems to be a much more primitive type, which did not necessarily derive from the Cordaitales.

Development of the hypopeltate scale.— The microsporophyll of the living *Araucaria muelleri* does not form an apical shield but a heart-shaped lamina attached in a more or less upright position to the stalk. Numerous pollen sacs are attached to the interior margin of the well-curved lobes. Although arranged somewhat below the stalk, they are obviously not attached to the lower surface of the lamina. If the basal lobes of the heart-shaped lamina would grow together below the stalk, the surface with its face toward the cone axis would represent the upper side of a peltate lamina. The sporangia attached to this side would be above and not below the leaf surface, which does not agree with Pilger's hypopeltate theory. The protective microsporangial scale of *Primaraucaria* and the paired sporangia, fused partially with the scale appears to represent a primitive type (pl. 6, fig. 5). A theoretical intermediate type is shown in plate 6, fig. 6, in which the bracket of the scale and sporangia became elongated and fused and the lamina of the scale reduced along the basal end of the stalk. At a later stage, the lateral proximal portion of the lamina became separated in a heart-shaped fashion, similar to that of *Araucaria muelleri*, which led to the third stage shown in plate 6, fig. 7, representing a peltate or hypopeltate shape, forming the imbricate and later the tile-like cone of the living *Araucaria*. Any directional change of the sporangia should be considered secondary.

The fusion and reduction of the female bract and the seed scale in the modern *Araucaria* is now a completely accepted view. It seems plausible that a similar modification has taken place in the development of the so-called hypopeltate microsporophyll in view of the disclosures of the primaraucarian male organs and in a lesser degree of *Austrotaxus* and *Araucaria muelleri*. Wilde's proposal (1944, pp. 25, 40) that the coniferous microsporophyll units are homologous with the seed scale complex, appears to be well founded. That the short stalk of the microsporophyll of

Primaraucaria or others indicates extreme reduction, remains a moot question, which will depend on the ultimate primitive form of the stalked sporangia. The stalk itself can be considered a purely structural support element.

THE FOLIATION OF *PRIMARAUCARIA*

Before details of the primaraucarian foliation components are discussed, some fundamental views of other investigators should be considered. Many supported the theory that leaves and sporangia are analogous elements, with the former taking a secondary position. Pilger and others believed in the sporophylls being modified leaves. The telome theory (Zimmermann, 1938) is today generally accepted, which claims the sporophylls derived from a vegetative system, branching in telomes. The latter bear the fertile organs. Phylloids form the varying leaf structure. It must be conceded that phylloids and telomic forms have in some later development become more closely related, fused and intergrown, so that distinction between them appears to be more difficult.

Florin (1945, p. 673) takes issue with the systematics of plants and their leaves in particular as expressed by Jeffrey (1902). Florin does not believe in the distinction of Jeffrey's macrophylls and microphylls. Zimmermann states that the macrophylly is derived from larger forced telomes, while the small leaves had their origin in smaller, less differentiated telome systems. The coniferous leaves also have been interpreted in various manners. Many writers such as Pilger, Goebel and others consider coniferous leaves as primarily macrophylls. from which the small uninerved leaves derived. Florin (1945, p. 684) distinguishes morphologically four types, of which the group of unforked leaves is known in all living conifers, while the bifurcated type (*Gomphostrobus*) is extinct.

Normal type of foliage.—Returning to the foliage of *Primaraucaria*, one is impressed by the variations of the leaves or leaf scales displayed on the same branch. When found separate, they could be easily mistaken for different species. Their general shape is convex triangular, rhomboidal to oblong. The scales of the female pericone are similar but more elongated and spreading. The bract scales of the female cone are longer and thicker, having a typical granular epidermis. The scales of the male pericone are more elongated than the leaf scales, being about twice as long, roundish at the apex and covered with numerous fine veins. The male bract scales are more roundish, curved, bilaterally-symetrical, some slightly forked and clasping.

Proliferous growth.—On plate 3, fig. 5 a proliferous development from the male pericone is shown. This growth is known in some living conifers, *Equisetum* and *Selaginella*, but is found also on fossil branches such as *Lebachia*. Burlingame (1913, p. 101, fig. 3) shows a staminate cone of *Araucaria brasiliensis*, which developed at the tip of the old strobilus two new cones and a foliaceous shoot. This rare assemblage suggests that proliferous growth may appear anywhere on the cone axis and it should not be unusual to find new shoots budding from the stem of a pericone. Only a few whorls of the proliferating primaraucarian pericone survived, but the leaves are typical of this genus, having characteristic cross wrinkles on the upper surface, so far only found on the foliage.

Sexfoliation.—An important distinction of some foliage branches found on *Primaraucaria* is displayed by the type of leaf borne on each of the two foliage spirals (pl. 6, fig. 13, pl. 3, figs. 2, 3). One type of the leaf is thick, having a coarse outer epidermis, while the leaf of the other spiral has an unusually smooth surface showing fine veins. It is about one-quarter shorter than the overlapping leaf of the first spiral and considerably thinner. The latter type may correspond with the scales of the male strobilus. The female scales of the seed-bearing cone may be represented by the longer, thick-walled foliage scales, which have a coarse epidermis.

Florin observed that the Cordaites are able to form single or multi-veined leaves in the same individual, the latter form characteristic of the vegetative region and the single vein type, predominant in the female flower. This condition is presumably reversed in some conifers. A still greater distinction of sexfoliate character is shown in the description of the coniferous form genus

Gomphostrobus Marion. It is characterized by a uni-nerved leaf forked at its apex. Although one genus is thought to have only the foliation represented by the forked type (*Carpentiera* Nemejc et Augusta), in others such as *Lebachia* (Florin, 1940, pp. 247–250, fig. 28) only certain branches are invested with forked foliage. Florin's restoration (fig. 28) is shown with a branch axis covered with forked leaves, while side branches of the last order have falcate leaves. Female cones originating from the same axis bear forked foliage leaves. Male cones, deriving from side branches disclose somewhat falcate leaves, or a slightly modified type. As already observed under similar conditions on the Cordaites, we find that the male cone of this *Lebachia* form has falcate, elongated, pointed leaves and the female strobilus more broad, clasping forked leaves. This arrangement is closely similar to the disposition of the dimorphic leaves of *Primaraucaria*, with the exception that this genus also discloses the two types of leaves, each confined to one of the foliaceous spirals of the same branch.

Troll (1938) explains heterophylly by the differentiation of the branch system into stronger and weaker components. Florin (1944, p. 385) believes that the forked foliage of the main axis and side branches is a juvenile form or transition between juvenile and following leaves. A parallel is drawn to the heteroblast of recent conifers, which is believed to be related to certain ontogenetic phases, following consecutively. None of these authors linked the difference of the leaves to sex-genetic causes.

Theory of sexfoliation.—The bifoliated character of numerous conifers confronts us with some problems which may reveal a closer relationship between normal and reproductive foliage. In the course of evolution of telomes and phylloids, a gradual approach of the leaves as protective and supporting structures for the reproductive organs can be observed. The so-called sterile and fertile leaves of some cordaitean inflorescences show the most primitive beginning in that group. The fusion of different leaf elements with the sporangial unit in some conifers of the Mesozoic testifies to rather early coördination of these components. Through the systematic development of branching and the fundamental functions of the biologically more adaptive foliage, which were apparent before the bisporangial reproductive organs developed, the need for support of the rigid sporangial structure, or its protection, became necessary. It must be accepted, that before bisexual reproduction developed, only one type of foliage was normal and, therefore, bifoliation was naturally a consequence of sex differentiation. Actually, the introduction of only one differentiated member was necessary, the one which supports the macrosporangia. This form modification was probably accompanied by physiological and anatomical ones.

The morphological differentiation of the leaves suggests that the two types of sporangia exacted the support of a leaf structure, which met the particular requirements of each group of sporangia. Therefore a modification of leaves took place before they reached their respective fertile organs. As the differentiation has thus far been observed only on branches or side branches of the last order, sexfoliation seems to be based primarily on the branch system. This is particularly proven by the *Lebachia* type of foliation, while in *Primaraucaria* some of the differentiation appears in the two types of foliage spirals, the extent of which on the branch is so far not known.

Thus we may distinguish two types of sexfoliation:

1. The dimorphic leaves arranged in spirals as in *Primaraucaria.*

2. The dimorphic leaves arranged on separate branches of the same axis as in *Lebachia.*

A third distinction may express itself in

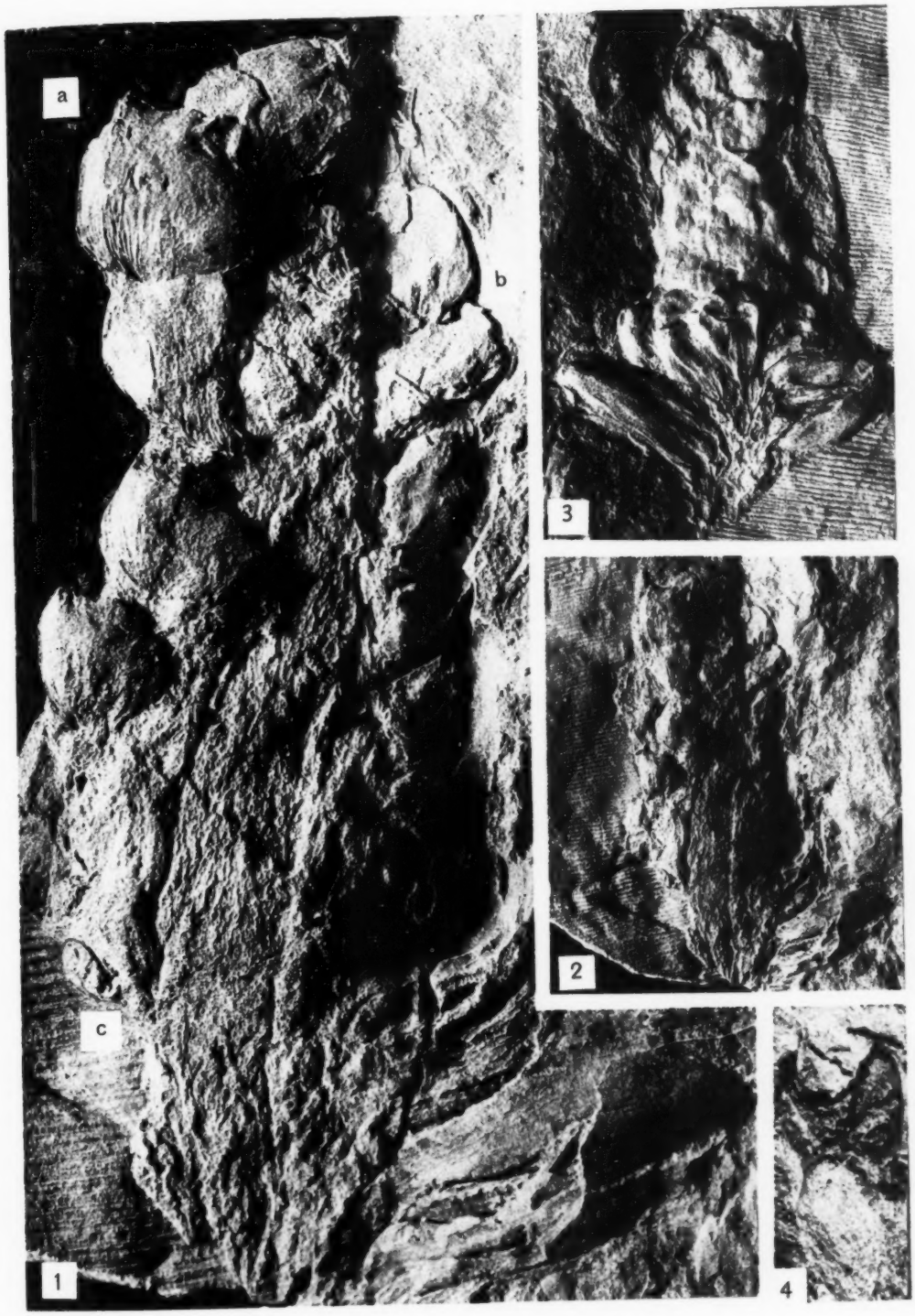
EXPLANATION OF PLATE 5

FIG. *1*—Male strobili of *Primaraucaria wielandi.* ×5. *a.* Bifurcated bract scale. *b.* Interior view of bract scale. *c.* Side view of immature microsporangia.

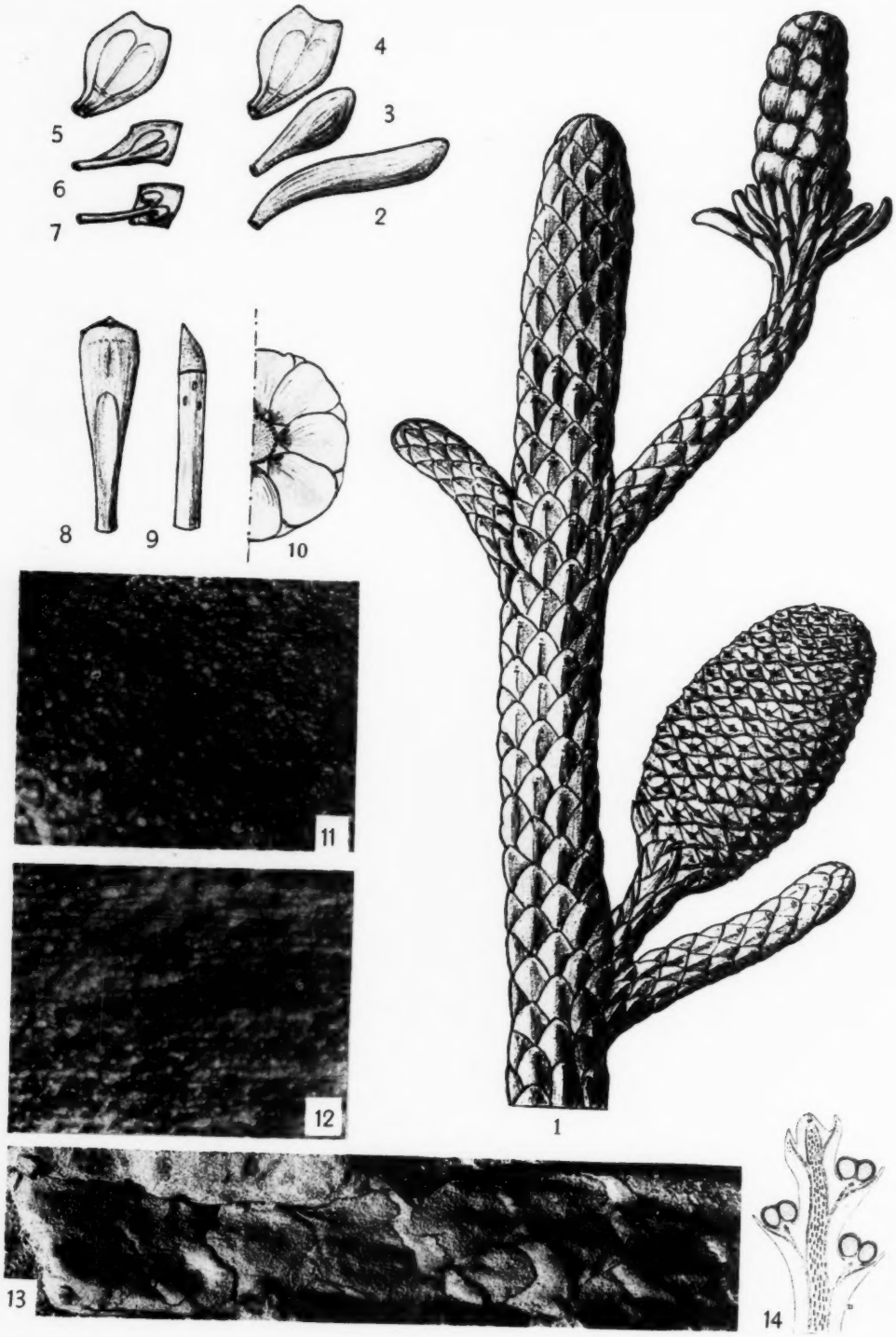
2—The same as fig. *1*, ×2.

3—The cast of the impression of fig. *1*, ×2.

4—Paired microsporangia in front view as in fig. *1c.* ×10.



Bock, Triassic *Primaraucaria*



Bock, Triassic *Primaraucaria*

the development of dioecious genera.

Sexfoliation of living plants.—The distinctness of dimorphous leaves on living species has not received, so far, sufficient attention. In some coniferous groups they are only survived by transition scales as in the Pinaceae, while pronounced foliage distinction is noticeable in the Taxodiaceae, particularly *Taxodium distichum*, *Sequoia sempervirens* and *Sequoiadendron giganteum*. In all three species the female cone grows on short-leaved side branches. There is a group of recent lycopods, *Selaginella*, some species of which have pronounced heterophyllous, alternating foliage. They are predominantly heterosporous and develop reproductive cones in which the sporophylls closely resemble in some species those of their heterophyllous foliage. As the genus *Selaginella* can be traced back as far as the Carboniferous, it would be interesting to find out how far its heterophyllous leaves correspond to any sexfoliate character.

SUMMARY

1. The genus *Primaraucaria* of the Upper Triassic of eastern North America, appears to be the earliest, distinct representative of the araucarian type of tree.

2. The female reproduction organs are typical araucarian cones; the seed unit consists of a solitary seed, borne on a seed scale, which is fused with a bract scale, both scales forming halves of a common rhomboidal apophysis.

3. The male strobilus of *Primaraucaria* has a thick conical axis, to which roundish, curved scales are spirally attached. The paired sporangia are fastened at the base to the integument of the cone stem and protected by the surrounding scale.

4. The strobili, particularly the male cone, are borne above a pericone, an aggregation of whorls of modified leaves.

5. The microsporophyll appears to be a primitive form, which may have been formed by the fusion of a bract scale and microsporangium.

6. Sexfoliation of the early conifers is based on heterophylly, representing two distinct leaf types, each closely coordinated with macro- or microsporophylls.

7. Two forms of sexfoliation are distinguished, of which the first type is arranged in two consecutive spirals on the same branch, while the second type is displayed on different groups of branches. Only two kinds of leaves are distinguished.

8. Sexfoliation, which can be traced back to the Cordaitales, may be represented by the Recent *Selaginella* as the first type, and by some Recent conifers as *Sequoia* for the second type.

REFERENCES

BURLINGAME, L. L., 1913, The morphology of *Araucaria brasiliensis:* Bot. Gaz., vol. 55, pp. 97–114, 2 pls.

DAUGHERTY, L. H., 1941, The Upper Triassic flora of Arizona: Carnegie Inst. Wash. Publ. 526, 108 pp., 34 pls.

EMMONS, EBENEZER, 1857, American geology: Sprague & Co., Albany, N. Y. 152 pp., 11 pls.

FLORIN, R., 1938–45, Die Koniferen des Oberkarbons und des unteren Perms: Palaeontographica, Bd. 85, Abt. B, Lief. 1–8, pp. 1–729.

——, 1950, Upper Carboniferous and Lower Permian conifers: Bot. Rev., vol. 16, pp. 258–282.

FONTAINE, W. M., 1883, Older Mesozoic flora of Virginia: U. S. Geol. Survey, Mon. 6, pp. 1–144, 53 pls.

JEFFREY, E. C., 1902, The structure and development of the stem in Pteridophyta and gymnosperms: Phil. Trans. R. Soc. London, Ser. B., vol. 195, London.

KENDALL, M. W., 1949, A Jurassic member of the Araucariaceae: Annales Bot., vol. 8, no. 50, pp. 151–161.

PILGER, R., 1926, Gymnospermae (in "Die na

EXPLANATION OF PLATE 6

FIG. *1*—Restoration of *Primaraucaria wielandi*. ×1.

2–4—Bract scale development of male strobilus from pericone scale. Fig. *2*, × about 2.

5–7—Presumable development of the hypopeltate microsporangium from fusion with the bract scale.

8—Female seed scale unit with seed indentation. ×2.

9—Young bract scale in female inflorescence. × about 8.

10—Attachment of scales in the male pericone.

11, *12*—Epidermis of foliage with obscure stomata. ×40.

13—Branch showing two consecutive spirals of sexfoliated leaves. (From branch shown in plate 3, figs. *1*, *2*) ×2.

14—Schematic longitudinal section of male strobilus of *Austrotaxus* (After Saxton).

türlichen Pflanzenfamilien") Engler und Prantl. Bd. 13, 446 pp.
SAXTON, W. T., 1934, Notes on conifers. The morphology of *Austrotaxus spicata* Compton: Annales Bot., vol. 48, pp. 411–427.
TROLL, W., 1938–39, Vergleichende Morphologie der höheren Pflanzen. Bd. 1: Vegetationsorgane. Berlin.
WARD, L. F., 1898–99, Status of the Mesozoic floras of the United States: U. S. Geol. Survey 20th Ann. Rep., vol. 2, pp. 211–748.
WILDE, M. H., 1944, A new interpretation of coniferous cones: Annales Bot., vol. 8, no. 29, pp. 1–41.
——, and EAMES, A. J., 1948, The ovule and "seed" of *Araucaria Bidwilli* with discussion of the taxonomy of the genus: Annales Bot., vol. 12, no. 47, pp. 311–326, 1 pl.
ZIMMERMANN, W., 1938, Phylogenie.—In "Manual of Pteridology." The Hague.

MANUSCRIPT RECEIVED OCTOBER 15, 1952

NOTICE

New officers of the Society of Economic Paleontologists and Mineralogists, elected by mail ballot, with terms beginning in April, 1954, are:

President: HANS E. THALMANN, Stanford, Calif.
Vice-President: FRANCIS J. PETTIJOHN, Baltimore, Maryland
Secretary-Treasurer: SAMUEL P. ELLISON, JR., Austin, Texas

During the same term H. N. Fisk will be first Past-President, C. C. Church second Past-President. J. L. Hough and Grover E. Murray continue as Editors for the Journal of Sedimentary Petrology and the JOURNAL OF PALEONTOLOGY, respectively.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 43–46, 4 TEXT FIGS., JANUARY 1954

CAMPYLOCYNODON PERSONI, A NEW OLIGOCENE CARNIVORE FROM THE BEAVER DIVIDE, WYOMING

ROBERT G. CHAFFEE
Dartmouth College Museum, Hanover, New Hampshire

IN the summer of 1950 a field party from the Dartmouth College Museum visited the Wagon Bed Spring area of the Beaver Divide, Wyoming. The purpose of the visit was not to collect fossils but to review the stratigraphy of the area. However, within the first hour of the party's arrival in the area Mr. Martin Person, a Dartmouth student, located the specimen that is the subject of this paper.

The material was skillfully prepared by Mr. William Fish. The illustrations are due to the combined work of Mr. Emil Rueb and Mr. Philip L. Martin.

Order CARNIVORA Bowdich
Suborder FISSIPEDA Blumenback
Family CANIDAE Gray
Subfamily AMPHICYNODONTINAE Simpson
Genus CAMPYLOCYNODON Chaffee, n. gen.

The name refers to the curved upper tooth row.

Genotype.—Campylocynodon personi, new species.

Generic diagnosis.—A small amphicynodont with M2/3. Skull short, especially in the basicranial region. Postorbital constriction narrow. Orbits large. Bullae large, close to midline, and with anterior end opposite the glenoid cavity. Preorbital region narrow, widening sharply posteriorly at P^3. Upper premolar three with a small but prominent protocone.

CAMPYLOCYNODON PERSONI Chaffee, n. sp.

The species is named for Martin B. Person, Jr., the discoverer of the type.

Type.—Dartmouth College Museum No. 50-26-6919, skull and jaws with upper cranium and right zygomatic missing, left zygomatic broken. Upper dentition—RP^1-M^2, LI^3-M^2; lower dentition—LC-M_3, RP_1-M_3. Atlas vertebra and an unprepared pes.

Horizon and type locality.—White River group, Chadronian stage, lower Oligocene. Southeast of Wagon Bed Springs, Beaver Divide, Fremont County, Wyoming. (NW ¼, Sec. 13, T. 31 N., R. 95 W.)

Specific diagnosis.—Same as for genus.

Description.—The skull is approximately the same size as *Mustelavus* Clark but is broader in proportion to its length and the facial region is shorter and narrower. The lower jaws are much like those of *Mustelavus* except that the condyle is higher, the ascending ramus is much higher and narrower, and, lastly, M_3 is present. It differs from *Paractis* Scott, the other small North American genus assigned to this subfamily (Simpson 1945), in that the lower premolars are much narrower and the whole jaw is slighter in *C. personi*. In appearance it resembles *Zodiolestes* Riggs (1942, p. 61; 1945, p. 96) except that it has no sagittal crest, the bullae are larger in comparison to the basicranial area, the anterior border of the internal nares is opposite M^2 rather than posterior to it as in *Zodiolestes*. Also *Campylocynodon personi* has a slight postorbital process on the jugal which is lacking in *Zodiolestes* and, in the lower jaw, the coronoid process is slender and extends well behind the condyle.

In the upper dentition, left incisor three is the only incisor preserved and it is so badly worn that little can be seen of its structure. The left canine, broken at the tip, is rather a small tooth in comparison to the size of the rest of the dentition and is quite round in cross-section. The first premolars of both sides are separated from the canines and from the second premolars by short diastemas. They are simple, single-rooted teeth. The second premolars are double-rooted with a slight indication of a cuspule forming on the posterior border. The third premolars are triangular in shape with a prominent cusp on the lingual side. They resemble the same teeth in the modern viverrid genera *Genetta* and *Herpestes*. It is possible that these teeth are the milk

FIG. 1—*Campylocynodon personi* Chaffee, n. gen., n. sp. Type, DCM no. 50-26-6919, ×1.1.

carnassials remaining in the jaw. However, there are no other indications of the animal having been a juvenile. The fourth premolar on each side has the usual high paracone with a short metastyle shear. Anteriorly there is a very small parastyle. The protocone is large, rounded and placed slightly anteriorly to the paracone.

The upper molars are wider than long and tend to be sub-quadrangular. On the first molar the paracone is the largest cusp and is placed quite near the antero-external corner. The metacone and protocone are smaller and more normally placed. On the antero-internal corner of the first molar on the left side there is a slight indication of a swelling or cingulum. Unfortunately, the same tooth on the right side is broken in this area and the presence of this swelling cannot be determined. The crowns of the second molars are so poorly preserved that only the shape can be seen.

The cranium is smooth, slightly inflated and gives no indication of a sagittal crest. The postorbital processes are prominent and the postorbital constriction is well defined. The orbit is large.

In the auditory bullae the posterior part (entotympanic?) of the sides and floor is missing, exposing the petrosal in the roof of the cavity. The remaining parts on both sides have the same conformation so it is improbable that the bullae were broken during burial. Either the entotympanic(?) was ossified and so loosely attached that it was lost after death or it was cartilaginous.

There is enough of the bullae left to show that they were well rounded antero-posteriorly, as in *Procyon* but with the anterior slope gentler. The anterior ends of the bullae are well in front of the postglenoid process, approximately on a transverse line through the middle of the glenoid cavity. Medially the bullae are rather close together leaving a narrow basicranium. The position of the posterior end is uncertain, though it probably was opposite the paroccipital process.

There is no indication that the bullae were divided into chambers, though this is not certain because of the loss of the entotympanic. The external auditory meatus seems to have been rounded and to have had much the same appearance as in *Procyon*, though there was no tubular meatus.

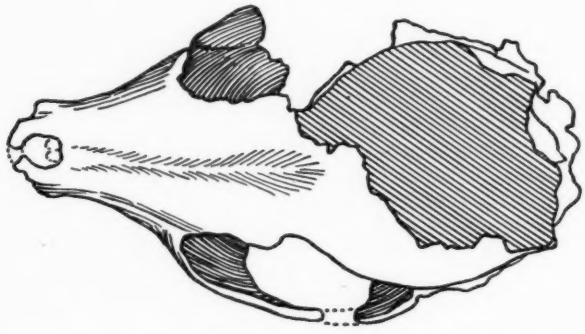


FIG. 2—*Campylocynodon personi* Chaffee, n. gen., n. sp. Type, DCM no. 50-26-6919, ×1.1.

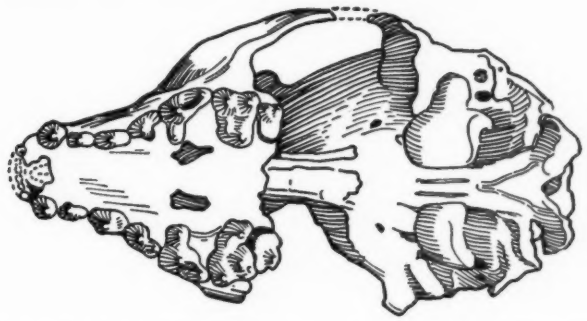


FIG. *3—Campylocynodon personi* Chaffee, n. gen., n. sp. Type, DCM no. 50-26-6919, ×1.1.

The promontorium is well exposed with its long axis at only a slight angle from the midline of the skull. Compared to the size of the bulla, it is larger than that of *Procyon* but of the same shape. The small fenestra cochleae opens postero-laterally and ventrally. The fenestra vestibuli, about the same size as the fenestra cochleae, faces directly laterally.

The foramen lacerum medium opens into the fossa ovale at the anterior corner of the bulla. It is divided from the opening for the Eustacian tube, lying slightly anterior and external, by a very small stylomastoid process. The course of the carotid canal seems to lie in the medial wall of the bulla running posteriorly and ventrally from the foramen lacerum medium. The posterior carotid foramen and the foramen lacerum posterium cannot be definitely located because of the missing entotympanic. The postglenoid foramen is small and is situated in a cleft formed between the postglenoid process and the tympanic. There is a foramen stylomastoideum definitivum on the mastoid process and it is connected to the foramen stylomastoideum primitivum by a groove lying posterior to the process pterygoideus.

An epitympanic recess and a fossa muscularis major are present in the roof of the tympanic cavity. A fossa, slightly larger than the epitympanic recess and lying lateral to it, appears to be the suprameatal fossa of Hough (1948).

On all the points mentioned above the auditory region compares closely with that of *Zodiolestes* as described by Hough (1944, pp. 473–476). The two genera differ in that the bullae of *Campylocynodon personi* are closer together, larger in comparison to the whole basicranial region and the mastoid process is smaller.

In the lower dentition the canine is small and slightly oval in cross-section with the long axis in the antero-posterior direction. There is a very small diastema between it and the first premolar, which is single rooted. The second, third and fourth premolars are quite narrow and increase in size and in posterior extension. The protoconid of the first molar is the highest cusp, slightly higher than P_4, and is connected to the paraconid. The metaconid is lower than either the proto- or paraconids. The talonid is smaller both antero-posteriorly and transversely than the trigonid and is basined with no indication of cuspules on the margin. The second molar is the same height as the talonid of M_1. It is longer than it is wide and subquadrangular in shape. The trigonid and talonid are of equal size and quite low. The third molar is present as a very small tooth only slightly larger than P_1.

The length of the lower tooth row is within the size range of *Pachycynodon tenuis* Teilhard de Chardin. The lower premolar series is comparatively shorter and the talonid of M_1 and the whole of M_2 are narrower than in *P. tenuis*.

The transverse processes of the atlas are broken so that the course of the canal for the vertebral artery cannot be deter-

FIG. *4—Campylocynodon personi* Chaffee, n. gen., n. sp. Type, DCM no. 50-26-6919, ×1.2.

mined. The atlas is very similar in size and shape to that of *Plesictis* (Hough, 1948, pl. 10, fig. 7).

Due to the poor preservation of the foot it was not prepared. As nearly as can be determined it is a left pes with only remnants of the tarsals remaining. There are three and possibly four metatarsals and an indeterminable number of phalanges. The metatarsals are long and closely compressed.

Relationships.—The specimen clearly belongs to the subfamily Amphicynodontinae Simpson (1945, p. 110) because of the large, medially placed protocone on P^4, the subquadriangular shape of the upper molars, and the comparatively large size of the talonid on M_1. The auditory region is procyonid in character, according to Hough (1948), in that there is a suprameatal fossa present, the carotid canal seems to lie in the wall of the bulla, and there is a foramen stylomastoideum primitivum present with an open groove for the facial canal. The dentition is procyonid only in the sub-quadriangular upper molars. There is no indication of a hypoconid or hypoconular shelf on P^4.

On the basis of the auditory region, Hough (1948) has assigned *Mustelavus*, from the Chadron formation, to the Procyonidae and has stated that *Plesictis* has a procyonid auditory region. The discovery of a "procyonid" auditory region in *Campylocynodon* would make it seem, as Hough (1944, p. 478) has suggested, that such an auditory region is primitive in carnivores. Therefore, unless an extremely vertical classification is used, the presence of a "procyonid" auditory region is not an absolute indication of membership in the Procyonidae.

Measurements, in mm., *Campylocynodon personi*, type, D. C. M. No. 50-26-6919.

Skull	
Total length	70.0
Condyles to preorbital border	48.2
Preorbital border to premaxilla	28.8
Breadth—at mastoid process	31.2
at postorbital constriction	14.9
at M_1	33.5
at P^3	17.9
at canine	11.8
Jaw	
Total length	49.4
Depth at M_1	7.5
Height at ascending ramus	23.5

Dentition

	upper	lower
C -L	3.0	3.0
W	3.0	2.8
P1 -L	2.8	2.2
W	1.9	1.8
P2 -L	4.0	4.1
W	2.4	2.4
P3 -L	5.4	5.0
W	4.0	2.5
P4 -L	7.0	5.2
W	6.0	2.8
M1-L	6.0	7.6
W	8.5	4.1
M2-L	3.4	4.0
W	5.3	3.0
M3-L	—	2.6
W	—	1.7
Cheek teeth	2.7	29.3

Metatarsal III—28.3
Metatarsal IV—27.9

MANUSCRIPT RECEIVED SEPT. 24, 1952

REFERENCES

CLARK, JOHN, 1937, The stratigraphy and paleontology of the Chadron formation in the Big Badlands of South Dakota: Ann. Carnegie Mus., vol. 25, pp. 261–350.

GREGORY, WILLIAM KING, and HELLMAN, MILO, 1939, On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: A phylogenetic study of the skull and dentition: Proc. Am. Phil. Soc., vol. 81, pp. 309–392.

HOUGH, JEAN R., 1944, The auditory region in some Miocene carnivores: Jour. Paleontology, vol. 18, pp. 470–479.

——, 1948, The auditory region in some members of the Procyonidae, Canidae and Ursidae: Bull. Amer. Mus. Nat. Hist., vol. 92, pp. 67–118.

LOOMIS, FREDERIC B., 1932, The small carnivores of the Miocene: Amer. Jour. Sci., 5th series, vol. 24, pp. 316–329.

MATTHEW, WILLIAM D., and GRANGER, WALTER, 1924, New Carnivora from Mongolia: Amer. Mus. Novitates, No. 104.

SIMPSON, GEORGE GAYLORD, 1945, The principles of classification and a classification of mammals: Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i–xvi, 1–350.

TEILHARD, DE CHARDIN, PIERRE, 1915, Les carnassiers des phosphorites du Quercy: Ann. Paleont., Paris, vol. 9, pp. 101–191.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 47–51, PLS. 7, 8, JANUARY 1954

A NEW LOWER CRETACEOUS STROMATOPOROID, *BEKHMEIA WETZELI* FROM NORTHERN IRAQ

R. G. S. HUDSON
Iraq Petroleum Company, London

ABSTRACT—The new genus and species of fasciculate stromatoporoid, *Bekhmeia wetzeli*, assigned to the Burgundiidae, is described. A summary of the stratigraphy of the type locality in the Bekhme Gorge of the Berat Dagh range is appended.

INTRODUCTION

THE limestone range of Berat Dagh (1700 m.) in Kurdistan, NE. Iraq, is a NW.-SE. anticline with the surface rock of Campanian-Maestrichtian Bekhme limestone.

It is crossed by the impressive Bekhme Gorge occupied by the Greater Zab River. The base of the limestone is a conglomerate and, unconformably below it, 916 m. of limestone and limestone-shale are exposed in the gorge and its immediate neighbourhood. This is divided, to a certain extent arbitrarily, into the Qamchuqa limestone (794 m.) above and the Chia Gara formation (122 m.) below: the former is mainly well-bedded limestone and is of Valanginian-Aptian age; the latter is mainly shale with limestones and is of Tithonian-Berriasian age. The specimens of the fasciculate stromatoporoid described in this paper were collected from the lower part of the Qamchuqa limestone.

The succession and fauna of the Qamchuqa and Chia Gara formations are as follows.[1] The division into stages is based on the rather rare diagnostic forms and on the comparison with the successions, both lithological and faunal, of other areas in Kurdistan which are more fossiliferous and therefore better dated. In the Bekhme Gorge succession the position of the boundaries between the various stages is, in the main, arbitrary.

[1] This brief account of the succession in the Bekhme Gorge is based mainly on the work of R. Wetzel of the Iraq Petroleum Company, Limited. Mr. Wetzel also collected the fossils, with the exception of those from the base of the section which were collected by the author and D. M. Morton. The ammonites were named by L. F. Spath and the Foraminifera by H. V. Dunnington and S. H. Smout. G. Cotton read the manuscript of the paper and made helpful suggestions. Permission to undertake the work and to publish it was given to the author by the Iraq Petroleum Company, Limited, who also made it possible for him to examine the Bekhme section. To all of these, and in particular to R. Wetzel, the author here expresses his sincere thanks.

PRE-MAESTRICHTIAN SUCCESSION, BEKHME GORGE

Qamchuqa Limestone

Upper dolomite.—106 m. thick. Light-grey, thin-bedded dolomitic limestones. No fauna.

Aptian.—82 m. thick. Bedded, grey or brownish-grey limestone with some shaly marl. Some chert and dolomitic limestone, abundant Foraminifera. The common fossils are *Exogyra* and *Orbitolina discoidea* Gras and var. *libancia* Henson. The only important diagnostic macrofossil is *Toucasia lonsdalei* d'Orbigny 1850 non J. de C. Sowerby 1836, occurring in some abundance about 25 m. above the base of the series. *T. lonsdalei* occurs in other sections in NE. Iraq, notably Qamchuqa and Sergulu, and in Iran, and is everywhere dated as Aptian. The type specimen of d'Orbigny's form is from the Urgonian (Tethyan facies of Barremian-Aptian) of Orgon, Rhône. It may be synonymous with *T. carinata* Matheron.

Lower dolomite.—76 m. thick. Massive-bedded dark-grey dolomitic limestones (bituminous). No fauna.

Lower Aptian.—164 m. thick. Dark-grey foraminiferal and shelly limestones. Occasional beds of nodular greenish marl, or fine-grained calcite mudstone. *Choffatella decipiens* Schlumberger and *Orbitolina delicata* Gras occur generally throughout. Otherwise the only diagnostic fauna is one of the *Heteraster oblongus* (Brongniart) group in the middle of the section. Such a fauna occurs in many Aptian sections in the Middle East

above a *Heteraster couloni* (Agassiz) fauna of Barremian age. It is possible that the base of the Aptian is higher in the succession than has been suggested here.

Barremian.—178 m. thick. Marly, nodular or shelly limestone, with occasional beds of dolomite. *Exogyra* common, other lamellibranchs, gastropods and terebratulids also occur. *Choffatella decipiens* occurs without *Orbitolina*.

Hauterivian.—88 m. thick. The upper 47 m. is a massive limestone with gastropods (*Nerinea*) and oysters. It also contains a marly nodular limestone, 2.25 m. thick, from which the stromatoporoids that are the subject of this paper were collected. The lowest of these beds contains a shelly fauna in which corals such as *Stylina* and *Stylosmilia* are not uncommon. The fauna is widespread in Kurdistan and forms a valuable marker within the Neocomian. *Pseudocyclammina*, probably *P. lituus* (Yokoyama), occurs and is a useful age-determinative form. *Choffatella decipiens* occurs sporadically throughout.

Valanginian.—110 m. thick. Bedded blue-grey argillaceous limestone with, in the lower part, an alternation of thin bedded limestone and shaly limestone containing ammonites and thin-shelled lamellibranchs such as *Pecten archiacianus* d'Orbigny var. The ammonite fauna is an hoplitid one and, though specific identification is not possible, it is considered by Dr. Spath to be probably Valanginian.

Chia Gara formation

Berriasian.—71 m. thick. Argillaceous limestones weathering yellow-brown, and marly shales. Contains throughout an ammonite and thin-shelled lamellibranch fauna including *Synoclonema orbicularis* (J. Sowerby) in abundance. Terebratulids such as *Zeilleria* cf. *tamarindus* (J. de C. Sowerby) and *Terebratula villersensis* de Loriol also occur. The upper beds contain *Neocosmoceras* aff. *peronatum* (Retowski), *Parodontoceras*, *Subthurmannia* aff. *boisierri* (Pictet—and *S.* aff. *occitanica* (Pictet).

The remaining beds contain the following:-*Paradontoceras* cf. *beneckei* (non Steuer) Mazenot, *Sarasinella*, "*Simberskites*," *?Spiticeras*, *Substeueroceras*, and *Thurmannites*. The "*boissieri*" fauna is widespread in Kurdistan towards the top of the Berriasian.

Tithonian.—51 m. thick. All Kurdistan sections show continuity of sedimentation between the upper Tithonian and the Berriasian. The Tithonian is not well exposed in the Bekhme area: it consists of hard grey marls with thin dark-grey limestone, the lowest 1.5 metres containing an abundant ammonite fauna of berriasellids indet., *Hectoroceras?*, *Paradontoceras* cf. *janus* (Retowski). This fauna is considered by Spath to be of uppermost Tithonian age, belonging to the "*permulticostatum*" zone of the *Substeueroceras* beds (Spath, 1950, p. 151).

SYSTEMATIC DESCRIPTION

Class HYDROZOA
Order STROMATOPOROIDEA Nicholson & Murie
Family BURGUNDIIDAE Dehorne
Genus BEKHMEIA Hudson, n. gen.

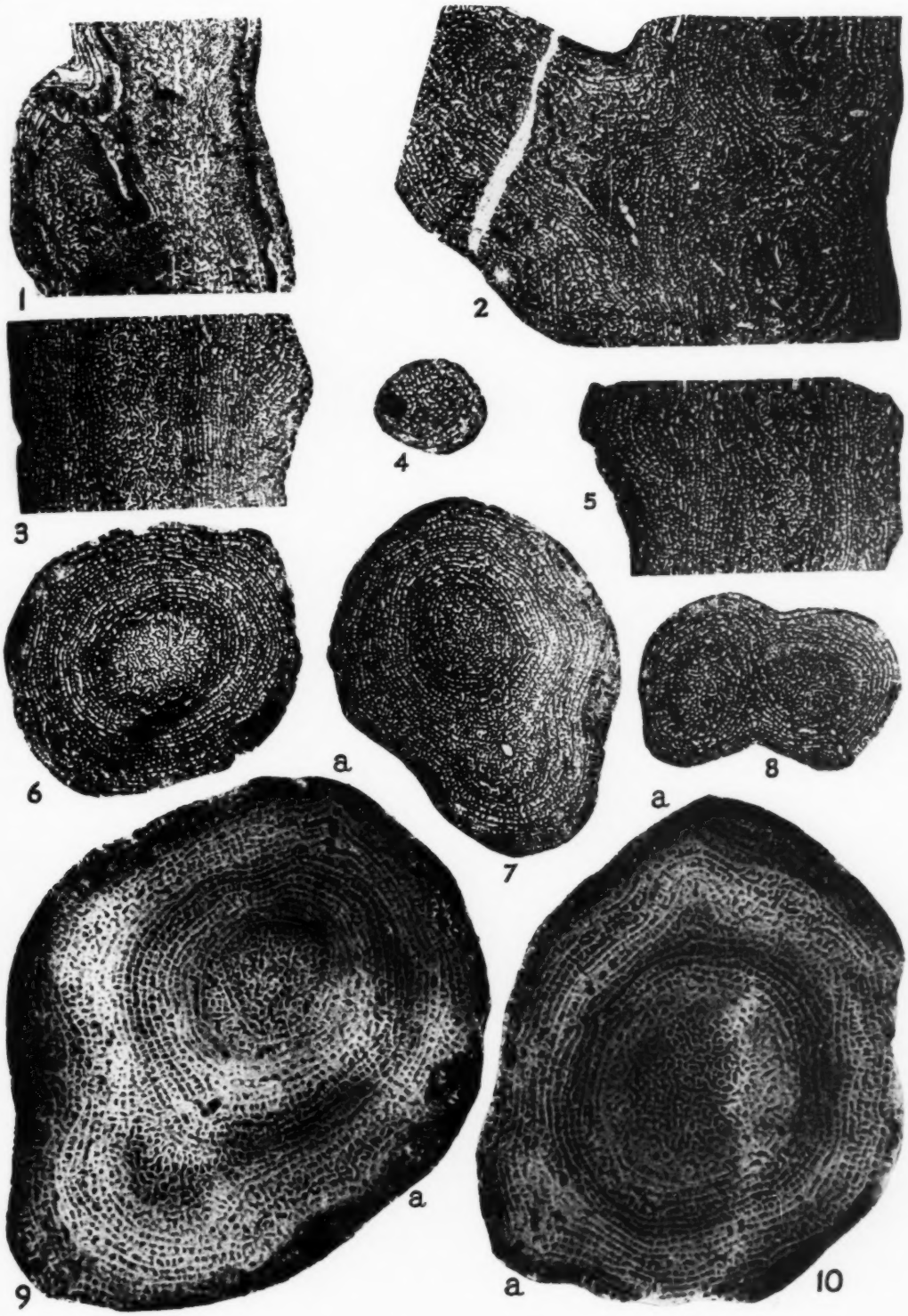
Type species.—*Bekhmeia wetzeli* Hudson, n. sp.

Diagnosis.—Coenosteum initially nodular, later fasciculate. Reticulum formed of continuous, thin, and regularly concentric thecal lamellae,[2] and interlamellar tubules

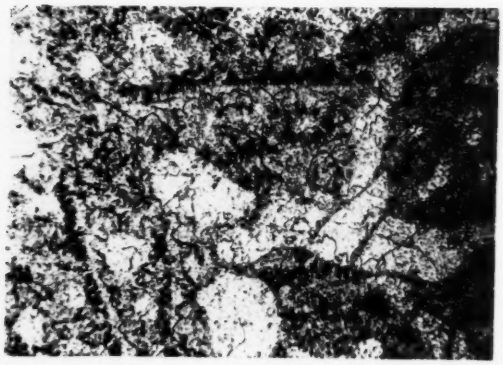
[2] Thecal lamellae are defined later in the description of the species.

EXPLANATION OF PLATE 7

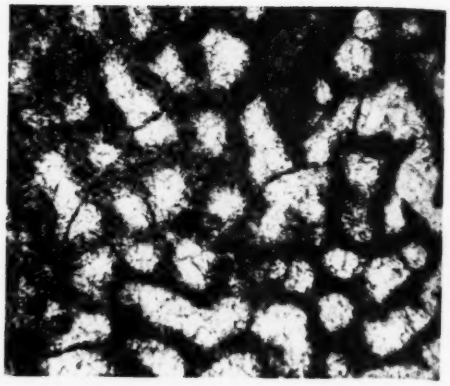
FIGS. *1–10*—*Bekhmeia wetzeli*, Hudson, n. sp., thin sections (*1–8*, ×3) and polished surfaces (*9*, *10*, ×5) of coenosteal branches (*3*, *5–7*, *9*, *10* from holotype; *1*, *2*, *4*, *8* from paratypes). *1*, axial longitudinal section showing new branch arising from axial zone of parent branch (H4442); *2*, tangential section of main stem and branches showing astrorhizae (H4431); *3*, axial longitudinal section showing axial and peripheral zones (H4429c); *4*, transverse section of young free branch (H4466); *5*, tangential longitudinal section showing, in centre, plan of structure between thecal lamellae (H4429a); *6*, transverse section showing axial and peripheral zones (H4430a); *7*, transverse section showing new branch (H4428a); *8*, transverse section across young parallel branches (H424b); *9*, medial polished surface showing astrorhizal tubes (a) (H4428b); *10*, polished surface 20 mm. below that of fig. *9* (H4430).



Hudson, Lower Cretaceous stromatoporoid



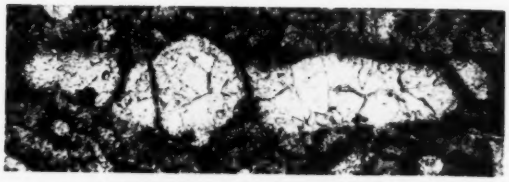
1



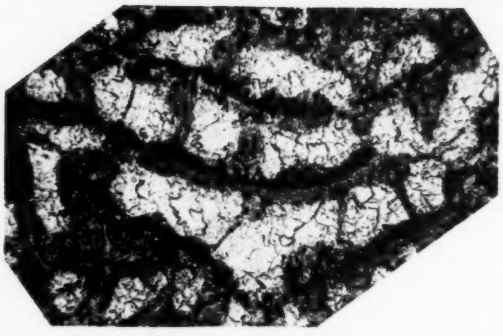
2

a

3

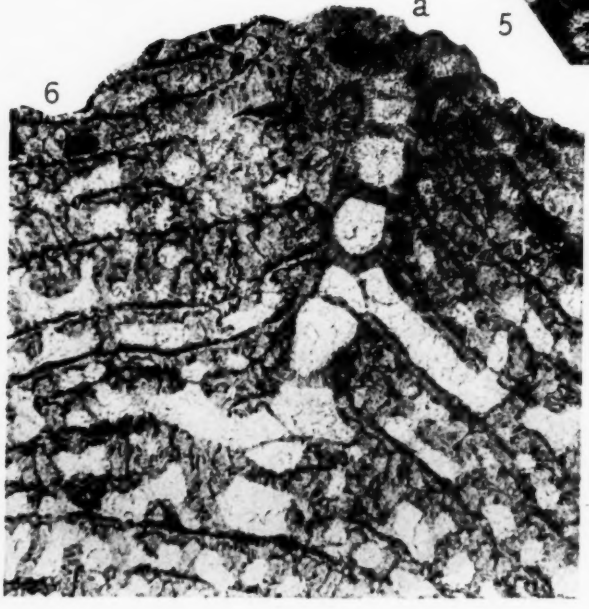


4



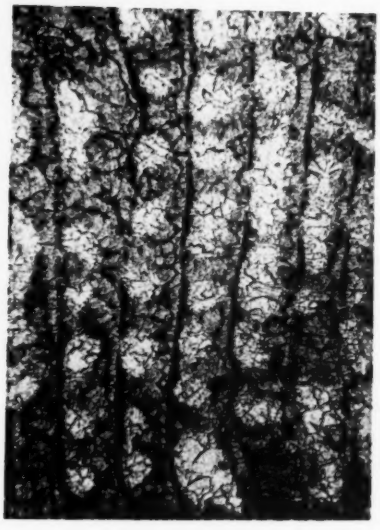
5

a



6

7



Hudson, Lower Cretaceous stromatoporoid

not vertically aligned. Reticulum of axial part of branch formed by vertical tubules, vermiculate in transverse section. Astrorhizae common, superposed and tabulate.

Distribution and horizon.—As for the type and only known species of the genus.

Remarks.—The genus is similar to *Burgundia* Dehorne (1916, Genotype *Burgundia trinorchii* Dehorne 1916: type from Portlandian of Vers, Tournus, France).[3] It differs from that genus in that the interlamellar structures are tubules and not branching pillars or laminae, and in that the reticulum of the coenosteal branch is differentiated into axial and peripheral zones.

The interlamellar structures of *B. trinorchii* consist of isolated pillars often joined to form laminae: rarely do they combine to form the walls of coenosteal tubules. *B. trinorchii*, according to Dehorne (1920), Steiner (1932), and Pfender (1942), lacks astrorhizae but possesses rare tabulate zooidal tubes ending in hillocks on the surface of the coenosteum (see Pfender, 1932, pl. xli). Similar structures in *B. semiclathrata* Hayasaka 1917 are accepted by Dehorne as simple astrorhizal tubes, and there seems no reason why they should not be so considered in *B. trinorchii*. Firtion (1940) figures a section of *B. trinorchii* showing a zooidal tube with lateral communicating canal, almost certainly a lateral astrorhizal canal. As astrorhizae are also common in *B. tutcheri* Kellaway and Smith 1938, their possession can be considered a diagnostic character of *Burgundia*, which therefore does not differ in that respect from *Bekhmia*. *Bekhmia* is included with *Burgundia* in the Burgundiidae, a family characterized by a reticulum dominated by thecal lamellae.

[3] *Burgundia trinorchii* Munier-Chalmas MS; *Burgundia trinorchii* Tornquist 1901, p. 1116; *Burgundia* Haug 1910, p. 931; are *nomina nuda* and neither the genus nor species as cited has any taxonomic significance.

BEKHMEIA WETZELI Hudson, n. sp.
Plates 7 and 8

Holotype.—Eight thin sections and the three remaining pieces of a coenosteal branch (H4428,[4] a, b; H4429, a-d; H4430, a, b; (Pl. 7, figs. 3, 5–7, 9, 10, and Pl. 8, figs. 12, 16, 17).

Paratypes.—(a) Parts of coenosteal branches: 45 specimens (H4414, H4422–27, H4431–68) including 15 thin sections (Pl. 7, figs. 1, 2, 4, 8 and Pl. 8, figs. 1, 4–5); 10 specimens (WL 2093/59–68) in collection of Geological Department, Iraq Petroleum Company, Limited; 10 specimens (WL 2093/10–19) in collection of Geological Department, Baghdad Museum. (b) Basal nodules: two sectioned specimens (H4415–21 and H4469, Pl. 8, fig. 3).

Locality of types.—Approx. 4.5 km. 54°E of N. of Bekhme, on mule track, left bank of Greater Zab River below junction with Rowanduz River. Map reference of Behkme: ZF 20873(E) 36200(N), ¼ in. sheet J. 38U (Rowanduz), Iraq. (Bekhme is approx. 58 km. north of Erbil, northern Iraq).

Horizon.—Qamchuqa limestone: Neocomian (Hauterivian).

Description.—Coenosteum fasciculate, initial branches arising from a basal nodule, which is irregularly spherical or ovoid. Branches cylindrical, slightly irregular,

[4] Numbers preceded by H are the registration numbers of specimens in the Department of Geology, British Museum (Natural History), London.

EXPLANATION OF PLATE 8

FIGS. *1–7*—*Bekhmeia wetzeli* Hudson, n. sp., thin sections (*1*, *2*, *4*, *5*, *7*, ×33; *6*, ×28) of coenosteal branches, and polished medial surface (*3*, ×1.3) of basal nodule: (*2*, *6*, *7* from holotype; *1*, *3–5* from paratypes). *1*, oblique section (outer part to left) of peripheral zone showing astrorhizal tubes and canals (H4426a); *2*, transverse section across axial zone showing tabulate tubes (H4430a); *3*, medial surface through basal nodule showing latilamellae and astrorhizae (H4469); *4*, transverse section through an astrorhiza of peripheral zone showing astrorhizal tube and lateral canals (H4431); *5*, longitudinal section through peripheral zone showing superposed lateral canals, astrorhizal tube to right (H4438); *6*, longitudinal section through mamelon showing superposed astrorhizae with lateral canals (H4428a); *7*, longitudinal section of peripheral zone (outer part to right) showing structure of thecal lamellae, lamellar lining, and pillars (H4429c).

slightly nodose, and from 2 to 20 mm. (generally about 10 to 12 mm.) in diameter. Length not known but branch fragments 10 cm. long have been collected. Branching by budding (not by dichotomy); branches usually in contact for a short distance though occasional ones develop normal to the main branch. Ill-defined mamelons (about 5 mm. across at base) are not uncommon and occasionally show possible astrorhizal canals. The surface is smooth or shows a finely vermiculate reticulum.

The skeletal structures of branch and basal nodule differ considerably. Each branch is sharply divided into axial and peripheral zones (Pl. 7, figs. 1, 3, 6): in the former, vertical skeletal elements, the coenosteal tubules, are dominant; in the latter, as in the basal nodule, it is the concentric skeletal elements, the thecal lamellae, that dominate the reticulum (Pl. 8, fig. 3). In the axial zone, the reticulum consists of vertical though sinuous coenosteal tubules with a fairly constant internal diameter of 100μ to 120μ, the tubule walls being generally from 50μ to 60μ thick (Pl. 8, fig. 2). In the outer part of the axial zone, the tubules bend outwards becoming approximately normal to the surface of the branch. In transverse section the tubules, if the walls are not unusually thickened, have no regularity: some are rounded and some tend to be polygonal (Pl. 7, figs. 6 and 7); many are elongate, due to incomplete walling, and flexuous, due to the sharp bending of the tubular walls. The walls are slightly thickened at the angles, suggesting that there they are vertical pillars, the remainder of the wall being formed by lamellar extensions from them (Pl. 8, fig. 2). In transverse section, the reticulum is thus markedly vermiculate. In longitudinal section (Pl. 7, fig. 1), the walls are seen to be irregularly sinuous so that they are often in temporary contact: individual tubes are thus comparatively short. The tubular walls have a minutely fibrous structure, the fibres radiating outwards from the axis of the pillar and from the medial plane of the lamellar extensions. The occurrence of tabulae in occasional tubules is discussed later.

In the basal nodule, growth upwards was more vigorous than in other directions, so that the thecal lamellae are concentric about a point near the base of the nodule; in the branch they are concentric about the axial reticulum. In both, the lamellae are thin (about 25μ thick), regular, and continuous, their distance apart, 200μ-230μ, being generally constant (Pl. 7, figs. 3 & 6). Coenosteal tubules similar to those in the axial zone occur vertically between the lamellae and are sharply defined from them. Their internal diameter is about 100μ-120μ, the tubular walls being about 60μ-90μ thick. In tangential section (Pl. 7, figs. 2, 5), the interlamellar tubules are seen to be markedly vermiculate: in longitudinal and transverse sections their walls appear as pillars normal to the lamellae (Pl. 7, figs. 3, 6). The tubular walls thicken outwards and, immediately under each thecal lamella, extend laterally to line its underside: this lamellar lining is in general slightly thinner than the tubular walls (Pl. 8, fig. 7). Latilamellae occur at regular intervals in the basal nodule but are less common in the branch.

The walls of the tubules of *Bekhmeia*, whether axial or interlamellar, are very finely fibrous, the fibres being perpendicular to the wall surfaces. This is similar in pattern to the radial structure of the Actinostromidae except that in that family there is a medial dark-coloured plane or axis. In *Bekhmeia* it is the outer parts of the walls that are darker, the medial part often being, in section, sharply defined as a light-coloured line. There is no trace of the fibrous "boutique" or "jet d'eau" of the Mesozoic Stromatoporidae or Milleporidiidae. The lamellar lining is similarly fibrous, the fibres being perpendicular to the lamellae.

The lamellae themselves, however, have a different microstructure. They are dark coloured, fibrous, the fibres being directed normally and outwards from the level base of a lamella. (See Pfender, 1937, pl. 4, fig. 5, showing lamella and lamellar lining). Their structure is comparable to that of the tabulae, the two skeletal elements being probably homologous. Their structure is thus different from the coenosteal lamellae, the horizontal skeletal elements found in other families of the Stromatoporoidea, which have a microstructure similar to that of the vertical skeletal elements. To distinguish between the two types, the concentric lamellae of the Burgundiidae are referred to

as thecal lamellae, a term expressing their function.

Though they have not been clearly recognized on the surface, thin sections show that astrorhizae are common both in the basal nodule and in the peripheral reticulum of the branches (Pl. 7, figs. 2, 9). The vertical tubules are superposed (Pl. 8, fig. 6), irregularly sinuous, about 200μ to 220μ in diameter, and of considerable length. Lateral tubes occur at intervals and may also be superposed (Pl. 8, fig. 5). Both vertical and lateral astrorhizal tubes may be irregularly tabulate and both may have a lining, vertically fibrous and about 20μ thick, which may independently cross the tube. The vertical tubes are not consistently normal to the thecal lamellae; they are sinuous and may cross them at an angle. And while the lateral tubes may be entirely interlamellar, this is not always so: they also may cross the thecal lamellae. Most astrorhizal tubes occur where the lamellae rise to form conical structures (Pl. 8, fig. 3), the mamelons of the surface.

Polished surfaces also show isolated tabulate tubes irregularly scattered in the lamellate reticulum (Pl. 7, figs. 9, 10; Pl. 8, fig. 3). These tubes have no regularity: they are not parallel to one another, nor regularly arranged with regard to the lamellae and tubules of the reticulum, which they cross haphazardly. The author is of the opinion that they are not "zooidal tubes" comparable to those of the Milleporidiidea or the Mesozoic Stromatoporidae, but that they are astrorhizal structures, mostly the lateral tubes.

The short and occasional tabulate tubes of the axial reticulum are not markedly different in diameter from the coenosteal tubules nor are they at variance with its normal pattern (Pl. 8, fig. 2). Yet they tend to be grouped and parallel to the outer surface, and the author considers them to be simple astrorhizae. Thus it is considered there are no zooidal tubes in *Bekhmeia* other than those of the astrorhizae.

A characteristic feature of *Bekhmeia* is its branching. *Burgundia ramosa* Pfender 1937 has coenosteal branches, but these apparently are independent growths or proliferations from a nodule—they do not apparently branch within themselves. Most of the branches of *Bekhmeia*, however, arose from other branches, some of the new branches remaining closely parallel to the parent branch, being enfolded within the peripheral zone; others apparently become rapidly free and continue as thin branches almost entirely composed of axial zone (Pl. 7, fig. 4); the whole coenosteum must have been a colony of closely packed parallel branches of no great height.

MANUSCRIPT RECEIVED JANUARY 29, 1953

REFERENCES

DEHORNE, Y., 1916, Sur un Stromatopore milléporoïde du Portlandien: C. R. Acad. Sci. Paris, vol. 162, pp. 430–433.

——, 1920, Les Stromatoporöidés des Terrains secondaires: Mém. Carte géol. France.

FIRTION, F., 1940, Sur la présence de *Burgundia trinorchii* dans le Portlandien de la région de Morteau (Jura): Bull. Soc. géol. France, ser. 5, vol. 9, pp. 161–162.

HAUG, E., 1910, Traité de Géologie, pt. 2, fasc. 2, p. 931. Paris.

HAYASAKA, I., 1917, On a new hydrozoan fossil from the Torinosu-limestone of Japan: Sci. Rept. Tôhoku Imp. Univ., ser. 2 (Geol.), vol. 4, pp. 55–59.

KELLAWAY, G. A., and SMITH, S., 1938, Stromatoporoids from the Inferior Oolite of southwest England: Quart. Journ. Geol. Soc. London, vol. 94, pp. 321–330.

PFENDER, J., 1932, Sur la présence de Stromatoporidés du genre *Burgundia* dans les calcaires portlandiens de Grand Corent, près Villereversure (Ain): Bull. Soc. Géol. France, ser. 5, vol. 1, pp. 739–742.

——, 1937, Quelques Hydrozoaires de la Syrie septentrionale: Notes Ht.-Comm. Syrie, vol. 2, 125–136.

SPATH, L. F., 1950, A new Tithonian ammonoid fauna from Kurdistan, Northern Iraq: Bull. Brit. Mus. (Nat. Hist.), ser. Geol., vol. 1, pp. 95–137.

STEINER, A., 1932, Contribution à l'étude des Stromatopores secondaires: Bull. Labs. Univ. Lausanne, no. 50.

TORNQUIST, A., 1901, Ueber mesozoische Stromatoporiden: Sitzb. k. preuss. Akad. Wiss. Berlin, 1901, pp. 1115–1123.

YABE, H., and SUGIYAMA, T., 1941. Discovery of *Circoporella semiclathrata* Hayasaka from Hokkaidô: Journ. Geol. Soc. Japan, vol. 48, pp. 38–42.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 52–58, PLS. 9, 10, JANUARY 1954

CAMBROPORELLA AND *COELOCLEMA*, LOWER CAMBRIAN AND ORDOVICIAN BRYOZOANS

MAXIM K. ELIAS
University of Nebraska

ABSTRACT—The fossil described by Korde (1950) as *Cambroporella tuvensis*, new genus and species, and erroneously interpreted by him as a syphonous green alga, is closely related to the Ordovician bryozoan *Coeloclema*, and is nearest to *C. crassimurale* of Baltic Province (W. Europe), and to *C. vaupeli* and *C. alternata* of America, which are here revised. The latter species and *Cambroporella* have in common the newly discovered spiral arrangement of zooecia in the "immature" (inner) part of the cylindrically curved elongate zoarium, but *Cambroporella* differs from the tubular *Coeloclema* by the abundant development of closely spaced zooecial diaphragms, and by the much smaller, apparently semitubular, elongately-oval, unbranched zoarium.

INTRODUCTION

EXTENSIVE geologic explorations in various parts of northern Asia conducted in the course of the last quarter of the century, resulted, among other contributions, in considerable progress of our knowledge of earliest Cambrian life. However, some of the biologic interpretations of the fossils new to science made by Soviet paleontologists are inacceptable. It has been already pointed out (Elias, 1950, p. 287, 298) that the genus *Chabakovia* Vologdin (1939) is not an alga, as he classified it, but apparently a foraminifer related to *Ptychocladia* from the Pennsylvanian of America;[1] and now it is necessary to remove from classification with algae another Lower Cambrian genus, *Cambroporella* described by Korde (1950).

The interpretation of *Cambroporella* as a bryozoan, which is now suggested, warrants this special paper about it, particularly in view of the fact that the spiral arrangement of tubular structures, detected on Korde's photograph, finds its counterpart in the similarly arranged zooecial tubes in *Coeloclema alternata*. Specimens of the latter species of this Ordovician genus have been studied with a view of verification of the hunch that *Cambroporella* could be a bryozoan, and it so happened that the detected spiral arrangement in the immature (inner) portions of the zooecial tubes in *Coeloclema alternata*, proved to be important in the conclusion reached on the bryozoan nature of *Cambroporella*.

[1] On the other hand, the supposed "Cambrian foraminifers of Jakutia," *Obruchevella* and other three genera, described by Reitling (Bull. Mosc. Soc. Nat., Dept. Geol., vol. 23/2, p. 77–81, 1 pl.) are erroneously so interpreted, and should be transferred to algae—a critical analysis of these will be given elsewhere.

HISTORY OF INVESTIGATION AND ACKNOWLEDGMENTS

About 4 years ago all scientific publications in the Soviet Union discontinued the previous practice of having abstracts in foreign languages, and even discontinued translation, in one of these languages, of the titles of the contributions or the titles of periodicals where they are being published. This move made more difficult the use of these publications abroad, and, because it seems desirable not to ignore them, it placed additional burden of deciphering the contributions in them on those who can read Russian, and so can inform their colleagues what these contributions are about.

Considering the limitations of time, I have concentrated on critical reading, and condensation or abstraction, of only those publications available to me, which deal with Paleozoic fossil invertebrates and plants, particularly Foraminifera, Bryozoa, Cephalopoda and Algae.

In the course of this work it became clear that serious errors have been committed by some of the authors. In some cases this happened because (1) some of them chose to ignore the pertinent and undoubtedly known to them American literature; and in other cases (2) seemingly because of overly narrow specialization. The example of the first group of errors is the erection of new sub-

genus of *Triticites* on a fusuline erroneously misidentified with *Alveolina montipara* Ehrenberg (1854), while failing to take into account the revision of the latter by Dunbar and Skinner (1936). Thus the new subgenus was named *Montiparus* (Rozovskaya, 1948), with Ehrenberg's species designated as genotype; but in fact, *Montiparus* Rozovskaya has nothing in common with the latter beyond superficial resemblance in shape and size (Elias, 1951, p. 36). A complete paper on this subgenus and various taxonomic implications, involving American and European fusulines, is being prepared jointly with Dr. Benjamin Burma, and in coöperation with Dr. Carl Dunbar and Dr. Maynard P. White. In the present paper a case in the second group of errors is scrutinized: an erroneous classification with algae (Korde, 1950) of a fossil that is most probably a bryozoan.

After reading the description and careful scrutiny of the published photographs of a fossil, which Korde (1950) named *Cambroporella tuvensis*, I have called this article to the attention of Drs. Ray S. Bassler, Roland Brown, and Vladimir Okulitch, for their judgment regarding possible relationship of *Cambroporella* to the fossils in their respective fields of specialization. Brown readily agreed that the fossil is not an alga, and Okulitch agreed that neither *Cambroporella*, nor the whole group of *Yakovlevia*, to the species of which it has some resemblance, should be classified with Pleospongia (Archaeocyatha. Because I requested some material of Ordovician *Coeloclema* in order to prepare properly oriented sections in order to match that of the holotype of *Cambroporella* published by Korde, through Dr. Bassler's help the U. S. National Museum kindly supplied bryozoan samples for my study.

As a by-product of the present investigation came about a new observation on *Coeloclema alternata* (James) from the Edenian of Cincinnati, Ohio, which indicates occassional spiral arrangement of its zooecia in the immature part of the tubular zoarium, a character previously not recorded for the species of the genus. It is particularly because of this spiral arrangement of zooecia that it became possible to interpret *Cambroporella* as a bryozoan with considerable degree of certainty, because the Cambrian form too shows a distinct spiral curving of the chambers, and this results in a strongly lopsided character of the deeper longitudinal sections of the zoarium. In nearly all other cylindrical or tubular Paleozoic Bryozoa, strict axial symmetry in all longitudinal and longitudinally-tangential sections is observed (except at the points of bifurcations).[2]

SYSTEMATIC DESCRIPTION AND DISCUSSION

Order CYCLOSTOMATA

Genus COELOCLEMA Nickles & Bassler

part 1878. *Ceramopora*, JAMES, Paleontologist, no. 1, p. 5.
1882. *Coeloclema*, ULRICH, Jour. Cincinnati Soc. Nat. Hist., vol. 5, nomen nudum.
part 1889. *Monticulipora*, JAMES & JAMES, Jour. Cincinnati Soc. Nat. Hist., vol. 11, p. 34.
part 1889. *Ceramopora*, JAMES & JAMES, Jour. Cincinnati Soc. Nat. Hist., vol. 11, p. 38.
part 1890. *Diamesopora*, ULRICH, Geol. Survey Illinois, vol. 8, p. 380, pp. 467–469.
part 1893. *Diamesopora*, ULRICH, Geol. Minnesota, vol. 3, p. 330.
part 1896. *Diamesopora*, ULRICH, in English edit. of Zittel's Text Book of Pal., p. 268.
1900. *Coeloclema*, NICKLES & BASSLER, U. S. Geol. Survey Bull. 173; pp. 24, 58, 76, 115, 211–212.
1911. *Coeloclema*, BASSLER, U. S. Nat. Mus. Bull. 77; pp. 50, 83–85.
1935. *Coeloclema*, BASSLER, Bryozoa (Foss. Catal., 1: Animalia, pars 67), pp. 16, 76.

Genotype.—Diamesopora vaupeli Ulrich (Nickles and Bassler, 1900, pp. 24, 211).

Ulrich introduced the genus *Coeloclema* in 1882, but left it without definition, a nomen nudum, and in 1900 abandoned its use, as he decided to place the Ordovician species of his *Coeloclema* in the Silurian genus *Diamesopora* Hall. However, Nickles and Bassler (1900) disagreed with this decision and revived *Coeloclema* for the same Ordovician forms for which it was originally intended.

[2] An undoubted case of exceptions is furnished by the spiral disposition of the zooecial tubes in the axis of *Rhombopora? spiralis*, from the Keokuk of Kentucky, on which Ulrich comments as follows (1890, p. 656): "The zooecia are arranged in a spiral manner about the axis of the branch. This is a very unusual feature among Paleozoic Bryozoa."

My attention was called to this case of spiral arrangement in a ramose species by Don Slama, when he worked, under my guidance, on some ramose Pennsylvanian Bryozoa for his M. Sci. dissertation at the University of Nebraska.

Because they defined the genus and indicated for its genotype the species which Ulrich described as *Diamesopora vaupeli*, they became thereby the legitimate authors of the genus, as per the International Rules of Zoological Nomenclature.

Although they indicated their belief that *Coeloclema vaupeli* is specifically identical with *Ceramopora alternata* James, they wrote their designation of the genotype in such way: "Genotype: *Diamesopora vaupeli* Ulrich = *Ceramopora alternata* James," that leaves no doubt that Ulrich's and not James's species is designated as the type, which is important if the two species are different, as now believed. James described and illustrated only those characters of his species which are observable externally, and he investigated neither the inner structure nor the epitheca. The distinction of *Coeloclema vaupeli* from *C. alternata* is indicated by the following:

(1) Ulrich describes and illustrates on three specimens the surface of *C. vaupeli* as "even" (1900, p. 468; pl. 41, figs. 4–4b), while James says that in *C. alternata* the surface is "sometimes with slightly elevated spots," which he shows also on the illustrations (1889, pl. 1, figs. 5–5b). (2) Ulrich describes the epitheca in *C. vaupeli* to be "nearly smooth," while in the specimens of *C. alternata* selected by Bassler for my investigation, the epitheca is distinctly wrinkled. (3) Maculae are mentioned by James for *C. alternata*, and indeed small maculae are occasionally developed in the specimens at my disposal (indicated by *x* on pl. 9, fig. 6), while Ulrich states emphatically that "in the absence of maculae it [*C. vaupeli*] resembles some of the Upper Silurian species of the genus," meaning here the Silurian *Diamesopora*. (4) The most important distinction of *C. alternata* is perhaps the spiral arrangement of the "immature" or initial portions of its zooecial tubules, a character not mentioned for *C. vaupeli* by Ulrich.

Indeed, it seems not entirely impossible that the material on which Ulrich established *C. vaupeli*, has the same features as just mentioned in *C. alternata*, only having them in a less distinct, or more sporadic development. These features in *C. alternata* are: the wrinkled epitheca, accompanied by the spirally arranged zooecial tubules, which are developed sporadically, and not throughout the branches of the zoarium; the small maculae, which are far apart from each other; and the surface elevations which are only locally developed. But it seems more probable that Ulrich's material, which comprises at least three fairly large fragments (see pl. 9 figs. 7–9), belongs to a species so closely related to *C. alternata*, that one could be considered a mere variation of the other. Be as it may, it is the presence in *C. alternata* of the spirally arranged zooecial tubules, sporadic as it may be, that compels its taxonomic recognition as a distinct species, and until the same feature is proved to develop also in *C. vaupeli*, the latter should not be considered conspecific with the former. However, the two species have much in common in the size, shape and spacing (in the mature part) of the zooecia, and in general build of the zoaria, which are tubular and ramose. The present investigation of the material identified as *C. alternata* by Bassler, results in the following characteristics of the species.

COELOCLEMA ALTERNATA (James)
Plate 9, figures 1–6; plate 10, figures 7–9

1878. *Ceramopora alternata*, JAMES, Paleontologist, no. 1, p. 5.
1889. *Monticulipora* (*Fistulipora*) *alternata*, JAMES & JAMES, Jour. Cincinnati Soc. Nat. Hist., vol. 11, p. 34, pl. 1, figs. 5–5b.
part 1900. *Coeloclema alternata* NICKLES & BASSLER, U. S. Geol. Survey Bull. 173, pp. 211–212.
not 1890. *Diamesopora vaupeli* ULRICH, Illinois Geol. Survey, vol. 8, p. 408, pl. 39, figs. 3–3b; pl. 41, figs. 4–4c.

Characteristics.—Zoarium tubular, ramose, bifurcating at about 13–14 mm. intervals. Outer diameter of the branches is usually from 3 to 4 mm., and the inner diameter about 2 to 2.5 mm. Branches tend to be uniformly wide, except for a length of about twice their diameter below a top point of bifurcation. External surface with occasional, irregularly distributed, broad and gently arching elevations. Axial lumen circular, occasionally excentric, its surface covered with thin (8 to 10μ) wrinkled epitheca (occasionally not preserved). When viewed in polarized light the epitheca blacks out as unit-crystal (Pl. 10, figs. 8, 9), which indicates its apparent homology to "germinal plate" or *lame germinale* (d'Orbigny) of

other fossil Bryozoa, and the "common bud" (Smitt, Borg) of the living ones. The wrinkles of the epitheca are perpendicular to the direction of the prostrate immature zooecial tubes, which frequently are spirally arranged. When becoming mature the zooecial tubes turn more or less abruptly outwards, their axes inclined at about 70°–80° to the zoarial surface. The walls between the immature parts of the tubes are thin, but become much thicker in the mature (outer) region, which is slightly more than two times as thick as immature region. Presence of lunaria seems only occasionally internally indicated by the development in the lower posterior angle of mature tubes of a narrow whitish strip, apparently equivalent to what Ulrich describes as "lunarium" made "of lighter colored material than the rest of the wall substance" in *C. vaupeli* (1890, p. 468); but no lunarial "hoods" could be detected over the apertures in *C. alternata*, and none were mentioned by James. Mesopores occur fairly constantly within the thick walls of the mature region, and the diameter of their lumen varies from 15 to 50μ; and occasionally one or two larger mesopores tend to occur in the angular areas between the neighboring apertures. Small elongated maculae are sporadically developed, their length varying from about $2\frac{1}{2}$ to 4 times the space occupied by a single ordinary aperture. Diaphragms generally absent, but at the abrupt bend from the immature to mature region, a well-developed diaphragm can be observed in the prepared longitudinal section (marked *a* on pl. 9, fig. 5).

Comparison.—The species differs from *C. vaupeli* chiefly by the occasional development of spiral arrangement of the immature zooecial tubes, wrinkled epitheca, feeble development of lunaria, and occurrence of small elongated maculae; the whole zoarium is also slightly more robust, the minimum width of branches in *C. vaupeli* being about two times smaller than in *C. alternata*. *C. alternata* differs from *C. crassimurale* Bassler by larger lumen of the zooecial apertures and their closer spacing; and by larger number and greater diameter of the mesopores. Perhaps the most important difference lies in the sporadic development of densely spaced septa in the mature part of the zooecial tubes, and, more frequently, in mesopores of the latter.

Genus CAMBROPORELLA Korde
CAMBROPORELLA TUVENSIS Korde
Plate 9, figure 12 (only)

part 1950. *Cambroporella tuvensis*, KORDE, Doklady Acad. Sci. USSR, vol. 73, pp. 371–374, fig. 1 only (not figs. 2 and 3).

Critical review.—Korde describes his fossil as a 15–16 mm. long, spindle-shaped jacket of a dasyclad alga, whose hollow axial part is shown in his reconstruction (Pl. 9, fig. 13) to occupy about half the diameter in its widest, up to 3–5 mm. diameter, middle part; and the outer part made of two-layered calcareous crust. He illustrates the fossil by two photographs of thin sections, one representing tangential and longitudinal sections of two individuals (Pl. 9, fig. 12), and the other a supposed transverse section of an individual (Pl. 9, fig. 10, here identified as *Yakovlevia*). In the latter two layers of the "jacket" are sharply outlined, indeed, their total thickness apparently varying from .04 to .05 mm. (which is slightly less than the measurements, given in the text, of the outer and inner layers of the jacket: .146–.23 mm., and .33–.46 mm. respectively). However, the hollow axial part, as seen in the transverse section (Pl. 10, fig. 10), is 2 mm. across the shorter axis, and 3 mm. across the longer axis of the ellipsis, and therefore the hollow part is actually occupying not $\frac{1}{2}$ but $\frac{2}{3}$ to $\frac{3}{4}$ of the diameter of the fossil, in its presumably widest part. However, Korde also illustrates (Pl. 9, fig. 12; his fig. 1) two more or less longitudinal (not axial or near-axial) sections of presumably the same fossil; and says that "In the upper left part of fig. 1 is seen [a part of] *central hollow*, which originally has been occupied by the axial part of the alga" (p. 372, my italics).

However, this is not what can be actually observed in the left upper part of Korde's fig. 1, which is by no means hollow, but has, on the contrary, clearly outlined complex structure as follows. It is made of a series of wider-than-high cells, which are stacked up like coins, in parallel to sub-parallel stacks which start as a bunch from lower left of the "axial part" (left center of fig. 12, pl. 9), and spread out upwards and to the right in a fan-like fashion. Each of the lower, most curved rows, terminates at the right edge of the fossil in a light colored body, next to which, in downward direction and in

close proximity to them, are the same kinds of bodies, called "pseudocells" by Korde, because supposedly being made by the prominences of the inner surface of the inner layer of the jacket. These lower "pseudocells" are somewhat irregular in outline and form diagonally crossing rows, which are said to belong to the "jacket around the axial thallus."

No matter how we interpret it, this photograph of the thin-section (which was selected as the holotype of the new genus and species) shows unbroken organic connection between the axial and the peripheral parts of a more or less elongately-oval fossil, both parts being clearly differentiated in a sort of a cellular structure; and there can be seen here no pronounced boundary between the axial and the peripheral parts suggestive of the supposed sharply expressed difference between them, and as seen, on the contrary, in the above mentioned cross-section of Korde's fig. 2 (present Pl. 10, fig. 10). Hence, only the two individuals pictured in Korde's fig. 1 truly represent his *Cambroporella*, the whole photographed slide being designated by him as the holotype. Therefore, interpretation of *Cambroporella* should not be in any way biased by the evidence of his fig. 2, which obviously belongs to a different fossil, as follows.

Yakovlevia.—The fossil of Korde's fig. 2 (present Pl. 10, fig. 10) is in all respects identical with *Jakovlevia tenuis* from the Lower Cambrian of Mongolia, as illustrated by Vologdin (1940, Pl. 31, figs. 4, 5), and this form may well be present in the limestone material from Tuva which Korde investigated. Vologdin places *Jakovlevia* in his family Rhabdocyathidae (1937) of Archaeocyatha, which interpretation is not a subject of the present investigation.

New interpretation.—That the right specimen of fig. 1 (present Pl. 9, fig. 12) represents more nearly tangential than longitudinal section, as compared with the left specimen, which shows in its upper part axial portion of a very similar individual—there seems to be no doubt, just as Korde concludes. However, the left section also clearly indicates that the individuals are not of spindle-shaped form, supposedly symmetrical about its longitudinal axis, but are distinctly lopsided internally, which could be somewhat reflected also externally. The left section shows that the curved cellular stacks are started on the left side, and traverse the whole width of fossil diagonally (though in somewhat varied direction), and with distinct upward curvature. This structure is so unlike that of dasyclad algae, that the latter interpretation seems quite untenable.

If not a dasyclad alga, then what? It

EXPLANATION OF PLATE 9

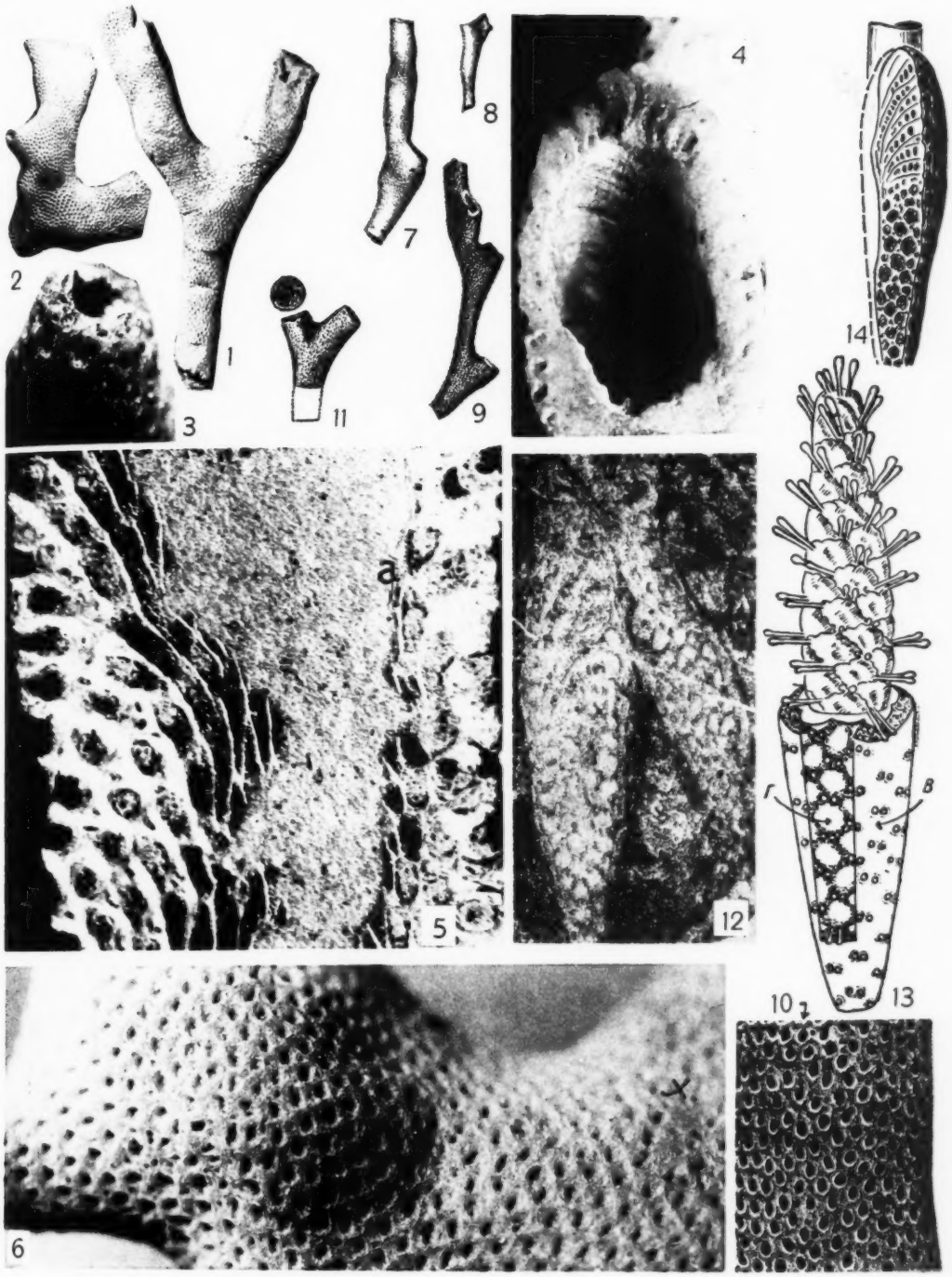
FIGS. *1–6*—*Coeloclema alternata* (James), topotypes from the Edenian (McMicken) of Cincinnati, Ohio. *1*, *2*—Fragments of zoarium, ×2. *3*—Detail from fig. *2*, showing growth tip of an embryonic lateral branch, probably arrested, ×20. *4*—View of the inner surface of the tubular zoarium, showing wrinkled epitheca, ×20. *5*—Thin tangential section prepared from the part of fig. *1* indicated by black arrow; to show spiral arrangement (left of the center) of the zooecial tubes in immature region. Compare with the corresponding spiral arrangement of curving tubes in tangential section of fig. *12* (upper left), ×20. *6*—Detail of the surface of fig. *2*, showing broadly convex elevation (left of the center) and small narrow macula (center of extreme right), ×20. All original. (p. 54)

7–10—*Coeloclema vaupeli* (Ulrich) from the Cincinnati group, Cincinnati, Ohio. All after Ulrich, 1890, pl. 41, figs. 4–4c, except enlarged ×10/9 from his drawings. *7–9*—Three examples, ×10/9. *10*—Detail of surface of fig. *7*, showing apertures with lunaria, and variably developed mesopores, ×10.

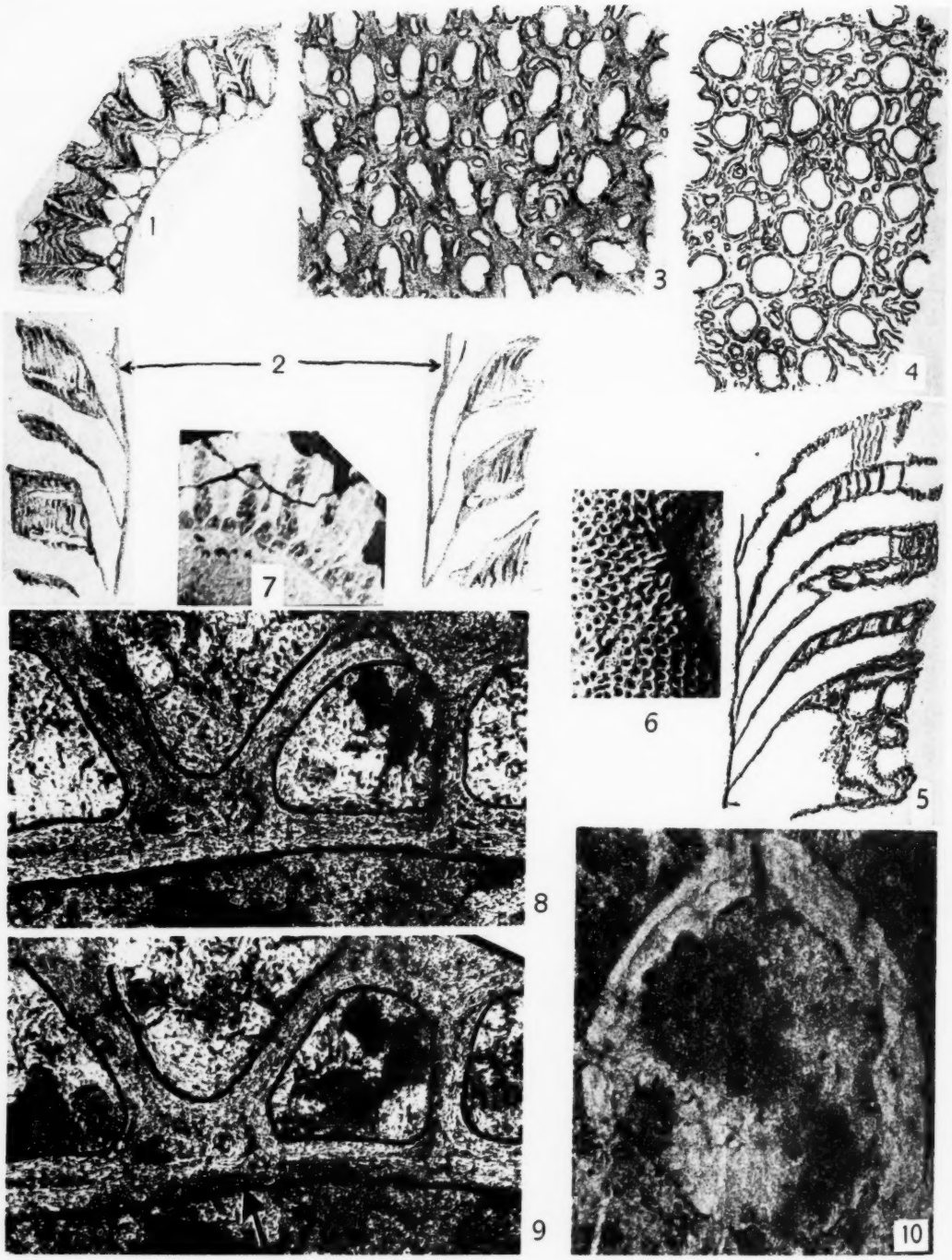
11—*Coeloclema crassimurale* Bassler from the Jewe ls., Ordovician of Baltic Provinces. Fragment of zoarium and end view of one of its branches, ×1. After Bassler, 1911, text.-fig. 24a (p. 84).

12, *14*—*Cambroporella tuvensis* Korde from the Lower Cambrian of Tuva, north-central Asia. Photograph of thin section indicated by Korde as "holotype"; left of the two sections in the slide (designated here as holotype) showing deeper axial cut of the zoarium above, and more nearly tangential cut of the same below; the cut of the right section is all tangential; ×5. After Korde, 1950, text-fig. 1, except enlarged to magnification indicated. *14*—Restoration of *Cambroporella* as a crustose bryozoan attached to a stem of alga (original). (p. 55)

13—Imaginary siphonous alga, based on erroneous combination of *Cambroporella tuvensis* (fig. *12* on this plate) and *Yakovlevia tenuis* (fig. *10* on plate 10). After Korde, 1950, text-fig. 3 (p. 373), ×6 (erroneously indicated on original drawing as ×3).



Elias, Cambrian and Ordovician Bryozoa



Elias, Ordovician Bryozoa and Cambrian *Jakovlevia*

seems that Korde was right in rejecting classification of this fossil with Archaeocyatha, and therefore relationships other than with them, or with dasyclad algae remain to be considered. After comparison with various organisms of the sea, affinity of the fossil with Bryozoa was decided to be most probable, and nearest to it among the satisfactorily described Paleozoic Bryozoa seems to be *Coeloclema crassimurale* Bassler (1911) from the Jewe limestone of the Middle Ordovician of the Baltic Provinces, and some American species of *Coeloclema*. Interpretation of the fossil as a bryozoan is strongly suggested by the general morphology and differentiation into axial (or immature) and peripheral (or mature) parts, so typical of most Paleozoic ramose Bryozoa; the outer and upward curvature and transverse septation of the parallel tubules; and the character and place of smaller tube-like elements between the larger tubules including their somewhat irregular tendency to develop in pairs. The latter can be easily interpreted as mesopores or larger acanthopores (or both), being much like the similar elements in a similar position in *Coeloclema*. All other mentioned elements in Korde's fossil and this bryozoan are comparable in form, position and dimension. The difference between them is only in the overall shape: zoarium of *Coeloclema* is cylindrical and occasionally branching, while that of *Cambroporella tuvensis* is supposedly spindle-shaped and not branching. However, this difference seems to be more apparent than real: the latter fossil, as was already pointed out, is not, in fact, axially symmetrical, as Korde erroneously concluded; nor is it spindle-shaped, but detracts from this shape at least in being not so internally, while externally its shape and size are very close to the smallest of the three specimens of *Coeloclema vaupeli* which Ulrich illustrated (Pl. 9, fig. 8). That is, instead of being a fusiform tube as Korde assumes, its shape could be merely unevenly inflated, with elongate alternating expansions and contractions, the narrowest contraction being near its base. Besides, the very close proximity to its left edge of the basal parts of the curved tubules (in the left upper part of Korde's left section) indicates, that the shape of the fossil is, in fact, not tubular, but more nearly like a much elongated and somewhat cylindrically curved cushion. Such a shape is suggested in the present reconstruction (Pl. 9, fig. 14), to supersede Korde's obviously incorrect reconstruction (Pl. 9, fig. 13).

It seems conceivable that *Cambroporella* encrusted a small stem of an alga, but without encircling it, while the tubular *Coeloclema* did encircle similar algal stems completely.

Revised characteristics.—If the suggested interpretation of *Cambroporella tuvensis* is accepted, it would be the first known bryozoan from the Lower Cambrian of the world, and its morphology becomes of particular scientific interest. It may be characterized as follows:

Zoarium in form of small, elongately crustose, more or less bilaterally symmetrical and unequally inflated cushion; about 15–16 mm. long, up to 3.5 wide, and about

---

EXPLANATION OF PLATE 10

FIGS. *1–3*—*Coeloclema vaupeli* (Ulrich), from the Cincinnati group, Cincinnati, Ohio. All after Ulrich, 1890, pl. 39, figs. 3–3b, except enlarged ×10/9 from his drawings. *1*—About one-fifth sector of a circular transverse section. *2*—Vertical (axial) section. *3*—Tangential section near surface of mature area. All ×20. (p. 54)

4–6—*Coeloclema crassimurale* Bassler, Ordovician of Baltic Provinces. All from Bassler, 1911, text-figs. 24b and 24c (p. 84), and pl. 7, fig. 12. *4*—Tangential section, "exhibiting the thickness of walls, obscure lunarium, and small, irregular mesopores," ×20. *5*—Vertical section through one side of a zoarium, ×20. *4* and *5* from the Jewe ls. *6*—Surface of a basal expansion from the Kuckers shale (C_2), from Esthonia, referred by Bassler to the species; ×4. (p. 58)

7–9—*Coeloclema alternata* (James), from the Edenian (McMicken) of Cincinnati, Ohio. *7*—About one-sixth sector of a circular transverse section, ×20. *8*, *9*—Detail of fig. *7*, showing the inner edge of the tubular zoarium, its epitheca blacking out in polarized light (fig. *9*, indicated by black arrow), ×480. All original. (p. 54)

10—*Yakovlevia tenuis* Vologdin from the Lower Cambrian of Tuva, north central Asia; erroneously identified as *Cambroporella tuvensis* by Korde, ×16.5. After Korde, 1950, text-fig. 2 (p. 373). (p. 56)

equally thick in its median part. Zooecial tubes start on its reverse, flush to about 10°–20° angle; but about half-way to the obverse they curve to nearly perpendicular orientation, and open up at its surface with about the same diameter. Their lumina are somewhat irregularly rounded, and of somewhat variable diameter: .5 to .8 mm., but tend to be more or less uniform in size and to be arranged into two systems of diagonal rows, whose angle of crossing is more or less in harmony with the bilateral symmetry of the zoarium. The thickness of the wall between tubules averages about .1 mm. in the immature region, and increases to about .2–.25 mm. in the upper half to two-thirds of the crust. Within the wall are developed subcircular (.16 mm. diameter) mesopores. The normal zooecial tubules have well-developed, usually closely spaced solid diaphragms, four to five per 1 mm. of length of tubule.

The whole zoarium is covered with a thin crust composed of semitransparent finely-granular "dark" calcium carbonate (Korde's "outer layer" of the "jacket"), which could be a combination of mineralized membrane and underlying coelomic layer, that stretched over the whole zoarium, except with small openings opposite the tubules. The spaces between the zooecial septa are filled by transparent calcite, much as is usually the case with petrified Bryozoa. The walls apparently are made of opaque material, as they are of somewhat lighter shade in the photograph fig. 12. Mesopores appear as subcircular dark spots (considered by Korde to be sporangia).

Comparison.—Cambroporella tuvensis is externally much like the smaller representatives of *Coeloclema vaupeli* (Pl. 9, fig. 8), except for being semitubular instead of tubular. Its zooecial tubules, when immature, are spirally arranged as in *Coeloclema alternata* (Pl. 9, fig. 5), while its profusely developed diaphragms are much like the diaphragms shown in some tubules and mesopores of *Coeloclema crassimurale* (Pl. 10, fig. 5). In all other respects it is also like *Coeloclema* and apparently represents a synthetic stock of early Cambrian age from which the Ordovician species of *Coeloclema* originated.

MANUSCRIPT RECEIVED JANUARY 20, 1953

It may be also mentioned that the densely spaced diaphragms in the mature area of *Cambroporella* resemble closely the similar development of diaphragms in *Idiotrypa parasitica* Ulrich from the Niagaran of Indiana, which Ulrich considered "a uniquely differentiated type" (1883, p. 273, Pl. xiii, figs. 1–1c.)

On the other hand, neither *Cambroporella* nor *Coeloclema* have much in common with *Archaeotrypa* Fritz (1947) from the Upper Cambrian of Alberta, which apparently belongs to a different circle of bryozoan affinity. Perhaps most characteristic of *Archaeotrypa* is the development of a puzzling zig-zag profile of every other of its longitudinal "walls."

REFERENCES

BASSLER, R. S., 1911, The early Paleozoic Bryozoa of the Baltic Provinces: U. S. Nat. Museum, Bull. 77, 382 p., 226 text-figs., 13 pls.

ELIAS, M. K., 1950, Paleozoic *Ptychocladia* and related Foraminifera: Jour. Paleontology, vol. 24, pp. 287–306, 2 text-figs., pls. 43–45. (Cambrian *Chabakovia* from Southern Urals interpreted as a foraminifer).

——, 1951, Moeller's error in identification of Ehrenberg's *Alveolina montiparus*, and the consequences (Abstract): p. 36, in Annual Meeting 1951: Am. Assoc. Petr. Geol., Soc. Econ. Pal. and Miner., Soc. Explor. Geophysicists. St. Louis, April 23–26, 1951, 74 p.

FRITZ, M. A., 1947, Cambrian Bryozoa: Jour. Paleontology, vol. 21, pp. 434–435, pl. 60.

——, 1948, Cambrian Bryozoa more precisely dated: Jour. Paleontology, vol. 22, p. 373.

JAMES, U. P., and JAMES, J. F., 1887–1889, On the monticuliporoid corals of the Cincinnati group, with a critical revision of the species: Jour. Cincinnati Soc. Nat. Hist., vol. 10, pp. 118–141 (1887); vol. 10, pp. 158–184 (1888), pl. 2; vol. 11, pp. 15–47 (1889), pl. 1.

KORDE, K. B., 1950, Dasycladaceae from the Cambrian of Tuva (northern part of Outer Mongolia): Doklady Akad. Sci. USSR, vol. 73, no. 2, pp. 371–374, 3 text-figs. (Russian).

NICKLES, J. N., and BASSLER, R. S., 1900, Synopsis of American fossil Bryozoa: U. S. Geol. Survey Bull. 173, 63 p.

ULRICH, E. A., 1882–1884, American Paleozoic Bryozoa: Jour. Cincinnati Soc. Nat. History: vol. 5, pp. 121–175, pls. 6–8; pp. 232–257, pls. 10, 11; vol. 6 (1883), pp. 82–92, pl. 1; p. 148–168, pls. 6, 7; pp. 245–279, pls. 12–14; vol. 7 (1884), pp. 24–51, pls. 1–3.

——, 1890, Paleozoic Bryozoa: Geol. Survey Illinois, vol. 8, pp. 285–688, 18 text-figs., pls. 29–78.

VOLOGDIN, 1940, Atlas of the leading forms of the fossil faunas of the USSR. Vol. 1: Cambrian. 194 p., 94 text-figs., 49 pls. (Russian).

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 59–66, PLS. 11, 12, JANUARY 1954

INTERNAL SHELL STRUCTURES IN THE MIDDLE CAMBRIAN GASTROPOD *SCENELLA* AND THE PROBLEMATIC GENUS *STENOTHECOIDES*

FRANCO RASETTI
Johns Hopkins University, Baltimore, Maryland

ABSTRACT—Internal shell structures are described for the first time in two species from Middle Cambrian strata (Mt. Whyte formation of British Columbia). The first species, assigned to the monoplacophoran gastropod genus *Scenella*, possesses six pairs of bilaterally symmetrical muscle scars, similar to those observed in Ordovician and Silurian members of the family Tryblidiidae, and justifies the assumption that it represents an ancestor of this gastropod group. The other species belongs to the problematic genus *Stenothecoides*, described as a crustacean but almost certainly not assignable to that class, here tentatively considered as a mollusk. While the external surface shows only growth lines, the inner surface is marked with a number of transverse, irregular, approximately paired ridges. The possible function of these structures and their bearing on the taxonomic position of the fossil are discussed. The type and another species of *Stenothecoides* are redescribed and illustrated.

IN A highly stimulating paper, J. Brookes Knight (1952) discussed primitive gastropods and their bearing on the phylogeny and classification of the class. The writer was induced to examine the gastropod material collected in his study of the Middle Cambrian formations of the Canadian Rockies (Rasetti, 1951), and observed internal shell structures deemed worthy of description.

Gastropods are not excessively rare in Cambrian deposits, but almost invariably the internal surface of the shell adheres to the matrix, so that only the external characters can be studied. Such features as growth lines or surface ornamentation may be useful for discriminating species and genera, but do not furnish any indication on the anatomy of the soft parts of the animal, hence are of but little use for understanding the evolution of the class. The oldest forms in which muscle scars or other internal markings were described are late Cambrian. Hence it seems interesting to report that such structures have been observed for the first time in an early medial Cambrian species.

Phylum MOLLUSCA
Class GASTROPODA Cuvier
Subclass ISOPLEURA Lankester
Order MONOPLACOPHORA Wenz
Family TRYBLIDIIDAE Pilsbry
Subfamily PALAEACMAEINAE Grabau and Shimer
Genus SCENELLA Billings, 1872
SCENELLA sp. undet.
Plate 12, figures 5–8

Available material.—Numerous individuals preserved in limestone, four of which show the interior structure.

Description.—This discussion is based on four individuals, of which the largest and best-preserved one (henceforth designated as specimen no. 1) was collected by the writer, while the other three (designated as specimens nos. 2, 3 and 4) were discovered in the U. S. National Museum collections. Specimen no. 1 is 15 mm. long, 13 mm. wide, and 5 mm. high. The other three shells are about 10 mm. long and 8 mm. wide, and proportionately somewhat higher. These four individuals are the only known ones which show the internal shell surface. Many more in the collections expose the external surface, showing poorly marked growth lines. Examination of collections from any one locality indicates variability in the relative proportions of length, width and height. In general, smaller individuals are proportionately higher. The shells have the shape of more or less regular cones, with the apex very slightly eccentric. For purpose of description, it shall be assumed that the position of the apex is anterior. Specimen no. 1

is the largest of all those observed. The described specimens are considered conspecific.

The structures are described as they appear on the internal cast, hence features described as depressions really were prominences of the internal shell surface, and vice versa. Specimen no. 4 is not an internal cast like the others, but a shell exposed from the internal side. The better to study and photograph its features, a rubber cast was made, and the description is based on it. All specimens are preserved in crystalline or oolitic limestone and show no flattening or distortion. The thickness of the shells is approximately 0.2 mm.

It is opportune first to describe the better-preserved specimen no. 1 (Pl. 12, fig. 5), then to indicate the features observed on the other specimens in the light of the information obtained from the first.

The structures visible on specimen no. 1 are: (1) Faint, irregular lines radiating from the apex. (2) A very shallow, indefinite furrow all around the shell, about 1 mm. inside the apertural margin, probably representing the impression of the sub-marginal thickening. (3) The muscle scars, to be described in detail.

There are six pairs of clearly visible muscle scars, arranged in bilaterally symmetrical pattern just inside of the intramarginal furrow. Two ideal lines (in horizontal projection) joining the apex to the scars of the first pair would form an angle of 160° with each other, with the vertex pointing backward. In other words, the scars of the first pair are located slightly in advance of a transverse line through the apex of the shell. The scars of the sixth pair are considerably closer to each other, the lines joining them to the apex forming an angle of 50°. This fact supports the assumption that the apex is anterior, as we may expect a wider gap between the scars corresponding to the cephalic part of the animal. The intermediate scars (conventionally numbered 2 to 5) are about equally spaced with the exception that the scars of the second and third pairs are anomalously close to each other on the left side, while being normally spaced on the right side. In view of other irregularities observed in the other specimens, this anomaly probably is an individual feature. Another possible exception to perfect bilateral symmetry is an inclination of the axis of maximum length of the shell with respect to the scar pattern; however, this fact cannot be definitely ascertained, as the margin of the shell is partly broken off.

Scars 1, 2 and 3 are each represented by a depression convex and sharply delimited toward the outside, extending inward and gradually fading out. In the scars of the first pair there are obscure indications of complex structure, more visible on the left side. Scars 4, 5 and 6 are considerably smaller, in form of oval or subcircular pits, and are not extended inward. On the left side of the specimen, they show definite indication of representing each two or three smaller scars joined together, but no such structure is visible on the right side, hence its significance cannot be assessed until more specimens can be studied.

In specimen no. 2 the apex is almost perfectly central, hence some doubt remains about the orientation of the shell. The photograph (Pl. 12, fig. 6) was mounted in the orientation which seemed more likely in view of the faint appearance of the scars 4 to 6 which, however, in this specimen are obscure and reveal no new features. Of the larger scars, only two pairs are clearly visible. Whether this is due to coalescence of pairs 2 and 3, as on the left side of specimen no. 1, or to lack of development of one of the pairs, could not be ascertained. One of the pairs is in advance, the other back of a transverse line through the apex. What can be seen of the scars indicates a perfect bilateral pattern.

In specimen no. 3, also an interior cast (Pl. 12, fig. 7), the posterior part is broken causing loss of most of the smaller scars. Two pairs of larger scars are visible on the left side, and two corresponding scars on the right side, with, in addition, a smaller scar interposed. These may represent pairs 1–3 on the right side, while it is possible that pairs 2 and 3 are fused on the left side, as in specimen no. 1. However, an interesting feature of this specimen is the presence of a pair of small, round pits considerably in advance of the apex, and farther inward from the margin than any of the scars previously described. The discussion of their

homology with the features of specimen no. 1 will be postponed until after description of specimen no. 4.

Specimen no. 4 is a shell exposed from the internal side and partly broken off, whose cast is illustrated on Pl. 12, fig. 8. The larger scars on the left side and all of the smaller, posterior scars cannot be clearly observed. The larger scars on the right side show the identical pattern as on the same side of specimen no. 3. In addition, there is the perfectly symmetrical pair of small, anterior pits forming, as in specimen no. 3, an almost exactly equilateral triangle with the apex of the shell.

It is possible that the differences observed between specimen no. 1 on one hand, and specimens nos. 2–4 on the other, are due to the presence of two different species; however, in view of the differences observed among specimens nos. 2–4, which were collected at a single locality and horizon, and also those between the right and left sides of the same individual, its appears more plausible to attribute the variable features to intraspecific variability. Perhaps the most important of these differences would be the lack of the anterior pits in specimen no. 1, the best preserved of all. However, it is possible that such pits existed in specimen no. 1. On the left side, a small depression is visible at the expected position and may represent the pit, if it is not due to an accident of preservation; while the position of the right anterior pit is covered by a patch of shell adhering to the internal cast. Only the study of a larger number of well-preserved individuals will allow a final decision on the homology of the scars in different specimens. However, even the scanty material available shows that the muscle scars in this species, as well as the external features, show considerable variability and some departure from perfect bilateral symmetry.

Horizon and localities.—All the specimens were collected from limestone of the upper Mt. Whyte formation (*Plagiura-Kochaspis* zone). Specimen no. 1 was collected by the writer at locality W4d (Rasetti, 1951): dark-gray, crystalline limestone 5 feet above base of unit 5 of Ross Lake section, 187 feet above base of Mt. Whyte formation; 0.2 mile NE of upper end of Ross Lake, Yoho National Park, British Columbia. The associated trilobites are *Amecephalus cleora* (Walcott), *Caborcella skapta* (Walcott), *Plagiura cercops* (Walcott), and *Schistometopus convexus* Rasetti. Specimens nos. 2–4 were collected by Walcott at USNM locality 58 k: upper Mt. Whyte formation (*Plagiura-Kochaspis* zone); Mt. Stephen, Yoho National Park, British Columbia.

Disposition of material.—Specimen no. 1: USNM 123374. Specimens nos. 2–4: USNM 123375.

Discussion.—It is opportune first to discuss the generic assignment of the above described form. The type species of the genus, *Scenella reticulata* Billings, is represented by excellent material and was redescribed and illustrated by Knight (1941). Topotypes in the USNM collections consist of limestone specimens showing the exterior, and internal casts in leached residue. The main differences between *S. reticulata* and the present form are: (1) The shell in *S. reticulata* is much thinner. This fact probably explains why the internal casts, carefully examined, failed to reveal any trace of muscle scars. (2) *S. reticulata* has a surface ornamentation of fine radiating lirae, totally absent in the species from the Mt. Whyte formation. (3) The shells of *S. reticulata* are not regularly conical like those of the present form, usually showing convex profiles, except near the margin where the profile becomes concave, the aperture flaring considerably in some individuals. However, these differences do not appear of generic value, especially in view of the extreme degree of variability observed in obviously conspecific samples of *S. reticulata.* The generic assignment is supported by the presence of forms similar to the present one in Lower Cambrian strata. For example, the Peyto limestone member of the St. Piran sandstone (*Bonnia-Olenellus* zone) in British Columbia carries a species (especially common at the writer's locality P22m = USNM locality 61d on Mt. Schaffer) which differs from the one here described chiefly in the proportionately greater height. All the specimens in the U. S. National Museum and the writer's collections were studied, but none were found showing the interior of the shell or its cast. The thickness of the shell in this Lower Cambrian species is intermediate be-

tween that of *S. reticulata* and the one here described. Walcott assigned both these Lower and Middle Cambrian forms to one species, *Scenella varians* Walcott, whose type, unfortunately, is a poorly preserved individual from the Lower Cambrian of Vermont. Until these gastropods are better understood and large populations can be examined to understand the limits of intraspecific variability, it seems better to refrain from either making new species or tentatively including forms of considerably different ages under the same name.

To evaluate the significance of the described muscle scars, it is opportune to compare them with those of other representatives of the order Monoplacophora, which includes bilaterally symmetrical, untorted gastropods provided with a single, conical shell. The discrete muscle scars observed in *Scenella* fully support Knight's assignment of the genus to the family Tryblidiidae, some of whose members show six pairs of bilaterally symmetrical muscle scars. Such scars were known in the Silurian genera *Pilina* and *Tryblidium*, the Ordovician *Archaeophiala*, and the late Cambrian—early Ordovician *Proplina* (Knight, 1952). The present discovery carries our knowledge of the muscle scars back from the latest late Cambrian to the earliest medial Cambrian; by analogy, we may rather safely assume analogous structures in the early Cambrian species of *Scenella*.

Comparing the muscle scars of *Scenella* with those of *Archaeophiala*, possibly the best known among the members of the family, we note certain differences. The scars of *Archaeophiala* are much more distinct, a feature obviously related to the great thickness of the shell in that genus; furthermore, with the exception of those of the anterior pair, they are more regular in size and the spacing is uniform, including the distance between the scars of the sixth pair which is equal to the distance between two successive pairs. The scars of the first pair are larger than the others and show compound structure, suggesting three pairs fused together. Similar characteristics are observed on some of the scars of *Pilina* and *Tryblidium*. Another feature of *Archaeophiala* is the presence of "shadow scars" accompanying the main scars; no such markings were observed in *Scenella*. All these differences, however, do not seem of great importance compared with the essential analogies of the bilateral symmetry and the basic number of six pairs of scars that is common to all the mentioned genera. Further study will be required to ascertain whether the anterior pits observed in some specimens of *Scenella* are muscle scars and to establish their possible homology with features of the later forms.

Phylum MOLLUSCA?
Class, order and family undetermined
Genus STENOTHECOIDES Resser, 1938

Supplementary description.—Shell small, univalve, fairly thick, suboval or subelliptical, elongated with the apex overhanging an end conventionally designated as anterior. Apertural margin approximately lying in a plane; shell moderately to strongly convex transversely. External surface marked with concentric, irregular growth lines. Internal surface with a number of irregular, transverse ridges on each side of the midline. Shell often asymmetric, with considerable intraspecific variation in shape and proportions.

Type species.—*Stenotheca elongata* Walcott (part).

Stratigraphic and geographic range.—Lower and Middle Cambrian of the Appalachian and Cordilleran provinces of North America.

Discussion.—Since the type species was never properly figured, and the generic description was based on the supposed affinity with *Stenotheca*, it appears worth while to illustrate the available material of this genus and rediscuss its possible relationships in connection with the internal structures described later in this paper.

Resser considered *Stenothecoides* as a crustacean on grounds that the writer holds totally invalid. The assignment is predicated, first on the assumption that *Stenotheca* is a crustacean, secondly that *Stenothecoides* is related to *Stenotheca*. *Stenotheca* is based on an English species, *S. cornucopia* Salter in Hicks. The English material was redescribed by Cobbold (1934) and a number of species from the Acadian Middle Cambrian were assigned to the genus by Matthew (1891, 1896). Both Matthew and Cobbold upheld the crustacean nature of *Stenotheca*, although Matthew successively

admitted different interpretations of the fossil. In 1891 he considered *Stenotheca* as a complete univalve carapace, whereas in 1896 he regarded it as one of the many plates of a cirriped. Cobbold shared Matthew's earlier opinion. Both authors considered the nature of the test, which Matthew described as extremely thin, punctate, and lacking growth lines, as the main reason for assignment to the crustaceans. The writer has not been able to examine authentic material of *Stenotheca;* however, whatever the systematic position of *Stenotheca* may be, there is nothing in the shell of *Stenothecoides* to suggest that this fossil is either related to *Stenotheca* or represents a crustacean. In fact, *Stenothecoides* differs from *Stenotheca* in the very features that were invoked to establish the crustacean nature of the latter: it has a thick, impunctate shell with well-marked growth lines. One seemingly unquestionable point is that the shell of *Stenothecoides* is the complete exoskeleton of an animal, which was obviously adapted for clinging to rocks like the recent limpets. Hence we may exclude reference to the cirripeds, the only crustacean group suggested by the thickness of the shell and the irregular growth lines. The Notostraca, and similar primitive crustaceans provided with a univalve carapace, were actively-swimming animals and the test was always very thin; furthermore, their carapace does not show growth lines, as it was shed at each moult. *Stenothecoides* most certainly was not a notostracan.

Poulsen (1932) figured specimens of *Stenothecoides* from the Lower Cambrian Ella Island formation of northeast Greenland. Apparently misled by the lack of bilateral symmetry of the shells, evidenced by the apex being turned slightly either to the left or to the right, he interpreted these organisms as bivalved and regarded them as undetermined lamellibranchs. It will be shown, in describing *Stenothecoides* cf. *elongata*, that this asymmetry of the apex does not indicate a bivalve shell. Hence assignment of the genus to the lamellibranchs is excluded. Resser (1938) named the Greenland form *Stenothecoides poulseni.*

Having disproved the crustacean or lamellibranch nature of *Stenothecoides*, the writer suggests assignment to an undetermined class of mollusks. Were the external features the only known ones, reference to the monoplacophoran gastropods would be strongly indicated by the appearance of the shell. However, the internal structures described in this paper seemingly indicate a fundamentally different organization of the animal from that inferred for *Scenella* and related forms, hence the assignment to the mollusks remains problematical. All that can be said in its favor is that reference to any other phylum is even less satisfactory.

STENOTHECOIDES ELONGATA (Walcott)
Plate 11, figures 3, 4

Stenotheca elongata WALCOTT (part), 1884, U. S. Geol. Surv. Mon. 8, p. 23, pl. 9, figs. 2, 2a; 1886, U. S. Geol. Surv. Bull. 30, p. 129, pl. 12, figs. 4a–b (not fig. c).

Stenothecoides elongata (Walcott) RESSER, 1938, Smithsonian Misc. Coll., vol. 97, no. 10, p. 24.

Available material.—Several shells in limestone, mostly poorly preserved and weathered.

Description.—Shells about 7 mm. in length and 3 mm. in width, fairly regularly oval or subelliptical, moderately convex, somewhat wider posteriorly. Growth lines well marked. Apex approximately symmetrical in the few specimens available.

Horizon and locality.—Middle Cambrian; Eldorado limestone (*Bathyuriscus-Elrathina* zone); USNM locality 55b, west slope of Prospect Peak, Eureka District, Nevada.

Types.—Lectotype and paratypes: USNM 15364.

Discussion.—Owing to insufficient material, it is not possible to form an adequate statistical concept of the species, as would be required for such variable organisms. The types fall well within the limits of intraspecific variability of the older form described below, which is not definitely assigned to *S. elongata* chiefly because of the considerable difference in age.

STENOTHECOIDES cf. S. ELONGATA (Walcott)
Plate 11, figures 6–10; plate 12, figures 1–4

Available material.—Numerous specimens well preserved in oolitic or crystalline limestone, collected by Walcott and the writer.

Description.—Shell averaging about 10 mm. in length, 5 mm. in width, and 3 mm.

in height. Shape highly variable, from almost regularly oval to markedly pointed anteriorly; sides often unequally convex. Posterior outline from regularly rounded to extended into a "tail," narrower than the median part of the shell and sometimes bent on one side. Apertural margin slightly thickened, lying in a plane. Apex sharply pointed, compressed laterally, at variable elevation above the anterior apertural margin and usually directly above it. Apex either symmetrical or pointing more or less to the right or left; all intermediate configurations occur in a suite of specimens from a single locality, making it impossible to separate right-handed and left-handed individuals and indicating fundamental bilateral symmetry of the shell. Growth lines always visible on outer surface; irregularly spaced coarser lines showing in some individuals.

One specimen is exfoliated and shows a good cast of the interior. No trace of growth lines on inner surface. Interior cast marked on each side with 15 to 18 transverse, fairly deep, somewhat irregular furrows separated from each other by about twice their width. Each furrow becoming gradually obsolete toward the median line, ending in the shallow marginal furrow that represents the impression of the thickened apertural margin. Some of the furrows showing a fairly sharp deeper impression near their midpoint. Furrows becoming gradually shallower, more irregular and sometimes confluent both toward the apex and the posterior end, thus making it impossible to establish the presence of a definite number. Shell 0.2–0.3 mm. thick; thin sections did not reveal canals or other significant structures.

Horizon and locality.—Common in the dark-gray, oolitic or crystalline limestones of the upper Mt. Whyte formation (*Plagiura-Kochaspis* zone) at several localities in British Columbia. *Stenothecoides* seems to be a good local index fossil for the zone. The figured specimens were collected by the writer (Rasetti, 1951) at the following localities: W4c′, W4d′, 160–187 feet above base of Mt. Whyte formation, 0.2 mile southeast of upper end of Ross Lake; W7f, 118 feet below top of Mt. Whyte formation, east of Kicking Horse Mine, on southeast slope of Mt. Field; and W9f, top 60 feet of Mt. Whyte formation, Fossil Gully, Mt. Stephen; all in Yoho National Park, British Columbia. Associated with the trilobites of the *Plagiura cercops* and *Fieldaspis furcata* faunules.

Disposition of material.—USNM 123376–8.

Discussion.—The internal structures of the shell consist of a somewhat indefinite number of transverse, narrow, prominent, approximately paired ridges and alternating furrows. Their function is of difficult interpretation. It might be assumed that they represent muscle attachments; in this case, the large number of muscle scars would suggest an animal differing in organization from the monoplacophoran gastropods, which possess six pairs of well-delimited muscle scars. The structures, however, may correspond to other anatomical features. Since they have no correspondence on the outer surface, it seems unquestionable that they accommodated some organs of the animal.

EXPLANATION OF PLATE 11

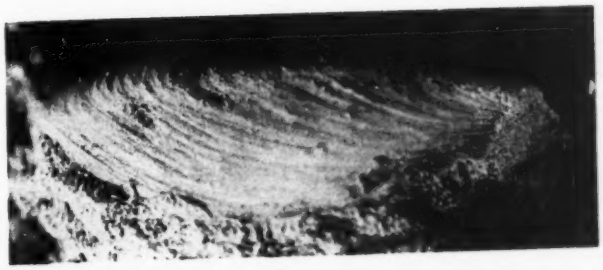
FIGS. *1, 2—Stenothecoides labradorica* Resser. Top and side views of lectotype, ×8; USNM 14883. Lower Cambrian, Forteau formation; Anse au Loup, Labrador. (p. 65)

5—? Stenothecoides labradorica Resser. Top view of specimen, ×8; USNM 96484, holotype of *Stenothecoides troyensis* Resser. Lower Cambrian, Schodack formation; Troy, New York. (p. 65)

3, 4—Stenothecoides elongata (Walcott), ×8. *3*, Top view of paratype; USNM 15364. *4*, Top view of lectotype; USNM 15364. Middle Cambrian, Eldorado limestone; USNM locality 55b, west slope of Prospect Peak, Eureka District, Nevada. (p. 63)

6–10—Stenothecoides cf. *S. elongata* (Walcott), ×5. *6*, Top view of an unusually short and wide shell (loc. W9f); USNM 123376. *7*, Top view of specimen (loc. W4d′); USNM 123377. *8*, Top view of another individual (loc W4c′); USNM 123377. *9*, *10*, Right side and top views of specimen (loc. W9f); USNM 123376. Middle Cambrian, Mt. Whyte formation; various localities in Yoho National Park, British Columbia (for description see text). See also Pl. 12. (p. 63)

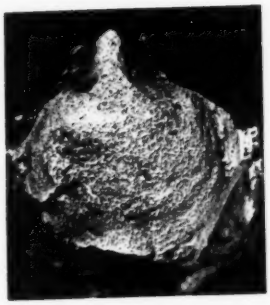
1



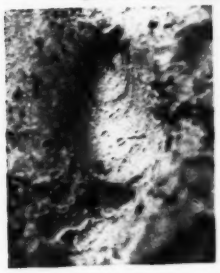
2

3

4



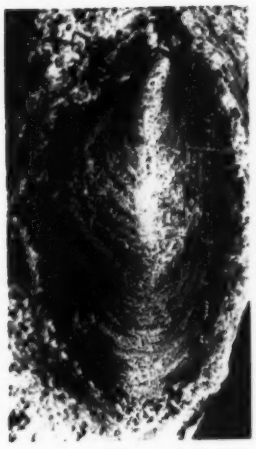
6



5

9

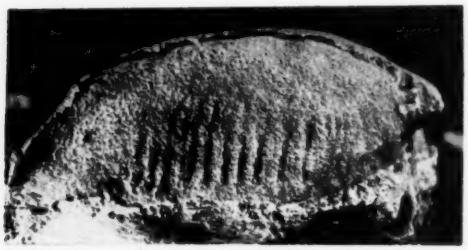
7



8

10

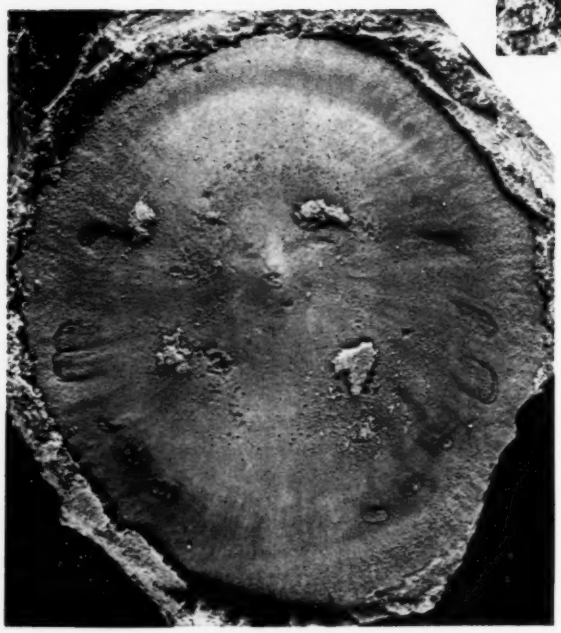
Rasetti, *Scenella* and *Stenothecoides*



1

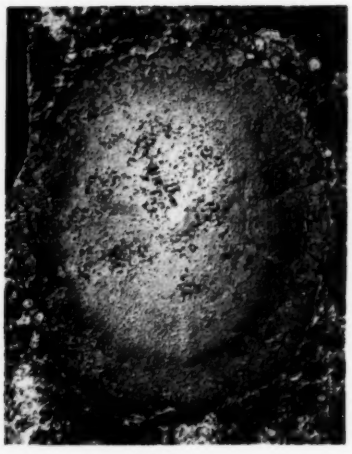
3

4



5

2



6

7

8

Rasetti, *Scenella* and *Stenothecoides*

Their approximate pairing suggests an organism with fundamental bilateral symmetry and, in addition, almost certainly excludes a bivalve shell with left and right-handed valves like those of the lamellibranchs and the conchostracans. The large number of ridges may indicate an animal with numerous segments, since it is possible that each ridge corresponds to a body segment. We may infer from the shape, thickness and structure of the shell that the animal was adapted for clinging to rocks and that the shell was not shed by moulting but grew by accretion at the apertural margin. The taxonomic consequences of this information were pointed out in the discussion of the genus.

STENOTHECOIDES LABRADORICA Resser
Plate 11, figures 1, 2

Stenotheca elongata WALCOTT (part), 1886, U. S. Geol. Surv. Bull. 30, p. 129, pl. 12, fig. 4.
Stenothecoides labradorica RESSER, 1938, Smithsonian Misc. Coll., vol. 97, no. 10, p. 24.
?*Stenotheca rugosa* WALCOTT (part), 1886, U. S. Geol. Surv. Bull. 30, p. 128, pl. 12, figs. 1d, 1e; 1891, U. S. Geol. Surv. Tenth Ann. Rept., p. 617, pl. 74, figs. 1h, 1i.
?*Stenothecoides troyensis* RESSER, 1938, Smithsonian Misc. Coll., vol. 97, no. 10, p. 25.

Available material.—A few shells well preserved in crystalline limestone.

Description.—Resser distinguished the species from *S. elongata* on the ground that: "*S. labradorica* is shorter and wider and the apertural margin is not as symmetrical as *S. elongata*. The growth lines are also somewhat weaker."

Largest shell 8.8 mm. long, 3.7 mm. wide and about 3 mm. high. Transverse profile almost flat at the sides, resulting in a fairly sharp keel along the median line. Shell rather pointed at the anterior end and somewhat more rounded posteriorly. Sides with unequal curvature, apex slightly asymmetric.

Horizon and locality.—Lower Cambrian (*Bonnia-Olenellus* zone); Forteau formation, Anse au Loup, Labrador.

Types.—Lectotype and paratypes: USNM 14883.

Discussion.—As far as can be ascertained from a few specimens in this genus of extreme intraspecific variability, *S. labradorica* seems separable from *S. elongata* not for the reasons mentioned by Resser (the ratio of width to length is the same) but for the keeled and more sharply pointed shell.

Stenothecoides troyensis is based on a single shell, here figured for comparison, of which all that can be said is that it problaby represents an immature specimen of *Stenothecoides*. As it seems useless to perpetuate a name attached to a specifically unidentifiable individual, the trivial name *troyensis* is here tentatively placed in the synonymy of *labradorica*.

ACKNOWLEDGMENTS

The writer is greatly indebted to Dr. J. Brookes Knight for reading the manuscript and offering valuable comments and suggestions. Thanks are also due to Mr. Ellis Yochelson for profitable discussions and for supplying photographs of specimens in the U. S. National Museum collections.

REFERENCES

COBBOLD, E. S., 1934, The Cambrian genus *Stenotheca:* Geol. Mag., vol. 71, pp. 463–468, pl. 23.
KNIGHT, J. BROOKES, 1941, Paleozoic gastropod genotypes: Geol. Soc. America, Spec. Papers, no. 32, pp. 1–510, 96 pls.

EXPLANATION OF PLATE 12

FIGS. *1–4*—*Stenothecoides* cf. *elongata* (Walcott), ×5. *1*, Right side view of specimen showing lateral furrows on internal cast; edge of shell is visible at the top, as the left side had not been exfoliated when the photograph was taken (loc. W9f); USNM 123376. *2*, Top view of same specimen; most of the shell has been removed except a portion near the apex. Note the strong asymmetry of the posterior part of the shell. *3*, Top view of specimen (loc. W9f); USNM 123376. *4*, Top view of another shell (loc. W7f); USNM 123378. Middle Cambrian, Mt. Whyte formation; various localities in Yoho National Park, British Columbia (for description see text). (p. 63)

5–8—*Scenella* sp. undet., ×5. *5*, Top view of exfoliated specimen no. 1, showing six pairs of muscle scars (loc. W4d); USNM 123374. *6*, *7*, Top views of exfoliated specimens nos. 2 and 3 (loc. USNM 58k); USNM 123375. *8*, Rubber cast of specimen no. 4, a shell exposed from the internal side (loc. USNM 58k); USNM 123375. Middle Cambrian, Mt. Whyte formation; various localities in Yoho National Park, British Columbia (for description see text). (p. 59)

——, 1952, Primitive fossil gastropods and their bearing on gastropod classification: Smithsonian Misc. Coll., vol. 117, no. 13, pp. 1–56, 2 pls.
MATTHEW, G. F., 1891, Illustrations of the fauna of the St. John group: Roy. Soc. Canada Trans. vol. 8 (1890), pp. 123–166, pls. 11–16.
——, 1896, Faunas of the *Paradoxides* beds in eastern North America, no. 1: New York Acad. Sci. Trans., vol. 15, pp. 192–247, 4 pls.
POULSEN, CHRISTIAN, 1932, The Lower Cambrian faunas of East Greenland: Meddelelser om Grønland, vol. 87, pp. 1–66, 14 pls.
RASETTI, FRANCO, 1951, Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains: Smithsonian Misc. Coll., vol. 116, no. 5, pp. 1–277, 34 pls.

MANUSCRIPT RECEIVED MARCH 24, 1953

NOTICE

A limited supply of some of the publications of the late Dr. G. H. Chadwick is available to interested persons. Please enclose postage when applying to Mr. Samuel G. Tuell, 39 Park St., Plainville, Connecticut for copies of the following:

Chemung stratigraphy in western New York. 1922
What is "Pocono?" 1935
Catskill as a geologic name. 1933
Summary of Upper Devonian stratigraphy. 1935
Discussion of "Cambrian and Ordovician geology of the Catskill Quadrangle." 1946
Geology of the Catskill and Kaaterskill Quadrangles. Part II: Silurian and Devonian geology. 1944 (1946)
Faunal differentiation in the Upper Devonian. 1935
Chagrin formation of Ohio. 1925
Ice evacuation stages at Glens Falls, N. Y. 1928
Chemung is Portage. 1935
History of value of the name "Catskill" in geology. 1936
Minerals of Mount Desert Island, Maine. 1943
The rocks of Mount Desert Island, Maine. 1943
The geology of Mount Desert Island. 1944
Genesee glacial lakes. 1924
Post-Ordovician deformation in the St. Lawrence valley, N. Y. 1915
Memorial to Herman LeRoy Fairchild. 1944

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 67–69, 1 TEXT FIG., JANUARY 1954

A NEW *PSEUDAELURUS* FROM THE LOWER SNAKE CREEK FAUNA OF NEBRASKA

J. R. MACDONALD
Museum of Geology, South Dakota School of Mines and Technology

ABSTRACT—A new species of *Pseudaelurus* from the Barstovian Lower Snake Creek beds of Nebraska is described. *Pseudaelurus aeluroides* n. sp. is the smallest known North American species. It most closely approaches the modern genera of felids because of the absence of the anterior premolars, the reduction of the diastema between the canine and P_3, and the progression of the premolars.

INTRODUCTION

THE cats, as well as the horses, beavers, and other forms from the later Tertiary, are beginning to present a progressively more complex problem in generic differentiation. New material is closing the gaps between the various well-established genera so that cases are constantly arising which require an arbitrary division between contiguous genera. The species described below could be considered the most primitive "*Felis*" or the most advanced *Pseudaelurus*. If we retain as the most important distinguishing characteristic the presence of a well developed talonid on the lower carnassial, then the cats possessing this character must be retained in the genus *Pseudaelurus* irrespective of other more advanced characters. While this may seem to be an arbitrary selection of a single characteristic for generic distinction it is becoming necessary that this be done. If this procedure is not followed we will be unable to avoid the intolerable confusion that would otherwise result.

My thanks are due to Dr. and Mrs. Harold J. Cook of Agate, Nebraska for making possible our collecting in the Sheep and Snake Creek localities, and to Dr. Edward H. Stevens who found the specimen herein described and presented it to the Museum of Geology.

DESCRIPTION

PSEUDAELURUS AELUROIDES[1] Macdonald, n. sp.

Type.—Right lower jaw, SDSM no. 5248. Partial right mandible with C, P_3, P_4, and M_1.

[1] Cat-like.

Type locality.—Northeast rim of Sinclair Draw, Sioux County, Nebraska.

Fauna.—Lower Snake Creek.

Age.—Upper Miocene, Barstovian.

Diagnosis.—M_1 with prominent talonid; metaconid lacking; carnassial notch open at bottom. P_4 with anterior and posterior accessory cusps subequal. P_2 and P_1 absent. Diastema between P_3 and C very short.

Description.—M_1 with long trenchant talonid; metaconid missing; protoconid larger than paraconid; carnassial notch open at bottom; no cingulum. P_4 with lingual side of talonid appressed to labial anterior corner of M_1; cingulum moderately developed around posterior accessory cusp; posterior and anterior accessory cusps subequal; principal cusp with apex above center of tooth, posterior and anterior blades symmetrical. P_3 broken. Cheek teeth crowded. Diastema between P_3 and C short. Canine ovoid in cross section with slightly trenchant posterior edge. Posterior mental foramen small, below posterior end of P_3; anterior mental foramen larger, below anterior end of P_3 and diastema.

Measurements (mm.).—

Canine, anterior-posterior diameter (at alveolar margin)	8.3
Canine, transverse diameter (at alveolar margin)	6.5
Diastema between Canine and P_3	7.3 ap.
P_3, greatest anterior-posterior diameter	9.4 ap.
P_4, greatest anterior-posterior diameter	11.4
P_4, greatest transverse diameter	5.4
M_1, greatest anterior-posterior diameter	15.6
Paraconid, greatest anterior-posterior diameter	6.7
Protoconid, greatest anterior-posterior diameter	6.7
Total length, M_1–P_3 inclusive	35.5

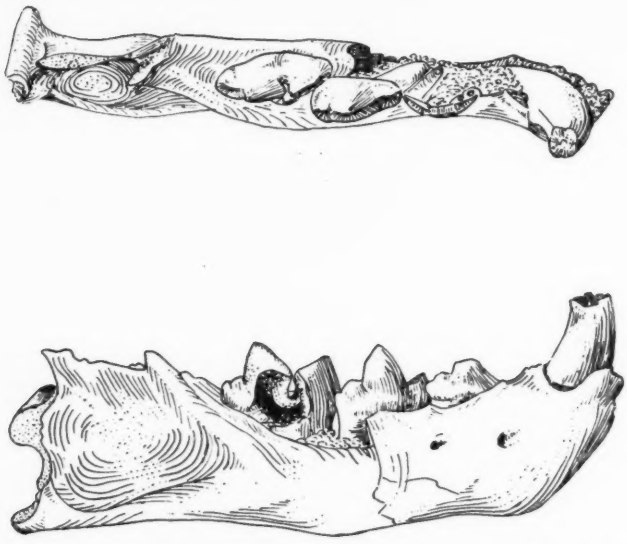


FIG. 1—*Pseudaelurus aeluroides*. Type specimen; occlusal and lateral views of right lower jaw, S.D.S.M. no. 5248. ×1.

Width of mandible below P_3	9.4
Width of mandible below M_1	9.6

Comparison with other species.—This species is much smaller than most of the other speces of *Pseudaelurus*. It shows no sign of P_1 and P_2 and has a greatly reduced diastema between the canine and P_3. Unlike *P. intrepedius* Leidy (1858), *P. aeluroides* has crowded dentition, no sign of a metaconid and the posterior cingular cusp on P_4 is almost completely lacking.

Pseudaelurus marshi Thorpe (1922) is larger, has stouter teeth, the accessory cusps on P_4 are more prominent and the principal cusp is not as high. M_1 has a pronounced metaconid and the paraconid is shorter-crowned with the crest of the blade more nearly paralleling the axis of the jaw.

Pseudaelurus martini (Hibbard) (1934) has a strongly developed talonid on the M_1 and a more open carnassial notch. As Hibbard (1934) points out, this form has a great many primitive features.

The large *Pseudaelurus thinobates* Macdonald (1948a) from the Black Hawk Ranch fauna has massive teeth, and the diastema between the canine and P_3 is very long.

Another Nebraska form from the Minnechaduza fauna, *Pseudaelurus pedionomus* Macdonald (1948b), has both the P_1 and the P_2; P_4 and M_1 are overlapping as in *P. aeluroides*, but P_3 and P_4 are not. The talonids of the M_1's are at about the same stage of reduction in both species.

CONCLUSIONS

Pseudaelurus aeluroides resembles the conditions found in modern cats more closely than any other described species from North America in the reduction of the Canine-P_3 diastema, the crowding of the cheek teeth, the lateral compression of the cheek teeth and the reduction of the accessory cusps.

In spite of its advanced characteristics, it is assigned to this genus because of the presence of a talonid on the lower carnassial. With the discovery of more and more conjunctive forms, it is necessary that some definitive character be chosen to represent the division between *Pseudaelurus* and "*Felis*." It is also true that the presence of a talonid, in conjunction with other characters, has been taken to be typical of *Pseudaelurus*. Therefore, in dividing the two genera, it is reasonable to establish the presence or absence of this character as the point of ultimate decision in spite of the other possibly more advanced characteristics.

LITERATURE CITED

HIBBARD, C. W., 1934, Two new genera of Felidae from the middle Pliocene of Kansas: Trans. Kansas Acad. Sci., vol. 37, pp. 239–255, Pls. IV–VI.

LEIDY, JOSEPH, 1858, Notice of remains of extinct Vertebrata, from the valley of the Niobrara River: Proc. Acad. Nat. Sci. Philadelphia, vol. 10, pp. 20–29.

MACDONALD, J. R., 1948a, The Pliocene carnivores of the Black Hawk Ranch fauna: Univ. California Publ., Bull. Dept. Geol. Sci., vol. 28, no. 3, pp. 53–80, 15 figs.

——, 1948b, A new species of *Pseudaelurus* from the lower Pliocene of Nebraska: Univ. California Publ., Bull. Dept. Geol. Sci., vol. 28, no. 2, pp. 45–52, 4 figs.

THORPE, M. R., 1922, Some Tertiary Carnivora in the Marsh Collection, with descriptions of new forms: Amer. Journ. Sci., ser. 5, vol. 3, pp. 423–455, 13 figs.

MANUSCRIPT RECEIVED NOV. 29, 1952

NOTICE

Dr. M. R. Sahni, Chief Palaeontologist of the Geological Survey of India, has recently written:

Some time ago we founded the Palaeontological Society of India to encourage and coordinate research in palaeontology, palaeobotany and prehistory in the universities and other institutions of this country. Among other objectives, such as to organise field work for the exploration of fossil localities and human fossil remains in India, publication of memoirs, etc., is the publication of a Journal.

Dr. Sahni adds the statement that presentation of publications, which will form the nucleus of the Society's library, will be greatly appreciated. They may be sent to him at the Geological Survey of India, 27 Chowringhee Road, Calcutta 13, India.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 70–75, PLS. 13, 14, JANUARY 1954

A NEW PERMIAN CRINOID FROM WESTERN AUSTRALIA

CURT TEICHERT
University of Melbourne

ABSTRACT—A new genus, *Jimbacrinus*, with *J. bostocki* as type species is described from Permian sandstones in the Northwest Basin, Western Australia. It is related to *Calceolispongia*, and for these two genera the new family Calceolispongiidae is proposed.

INTRODUCTION

IN 1949, the writer described the evolution of *Calceolispongia*, a remarkable crinoid from the Western Australian Permian province (Teichert, 1949), but in spite of the large number of specimens available the systematic position of the genus remained in doubt. During field work in the Northwest Basin of Western Australia in 1949, however, many specimens of a new crinoid genus were obtained which is so closely related to *Calceolispongia* that the two must be placed in one family. The new genus which supplies information regarding the anal structures that was not available from *Calceolispongia*, is here described as *Jimbacrinus*, with *J. bostocki* as the type species. The new family Calceolispongiidae is proposed for the two genera under consideration.

Although little can be stated about the stratigraphical position and range of *Jimbacrinus* it seems important that this genus should be made known, so that its fossil remains may not be confused with those of any of the numerous species of *Calceolispongia* which occur in the same district and which have proved important index fossils.

I am greatly indebted to Mr. J. Bostock, manager of Jimba Jimba Station, who discovered the locality of these new crinoids and in whose honour the type species has been named. The collections were obtained on field work organized by the writer for the Bureau of Mineral Resources, Geology and Geophysics, and I wish to record my thanks to Messrs. G. A. Thomas and C. Prichard, Geologists of the Bureau, for their assistance in securing this interesting material.

DESCRIPTION

Family CALCEOLISPONGIIDAE Teichert, n. fam.

This new family is here proposed for the genera *Calceolispongia* Etheridge, 1915, and *Jimbacrinus* Teichert, n. gen., with the following diagnosis:

Large dicyclic crinoids with slender stems and atomous, uniserial arms; structure of anal region simple, one anal plate (radianal) in cup; presence of calcareous tegmen known in *Calceolispongia*, of small anal sac in *Jimbacrinus;* five infrabasals; basal plates bulky, nearly always spinose, and in most species produced into long and heavy processes; radial plates, radianal, and first two brachial plates generally more or less strongly spinose, or at least tuberculate; radial facets occupying full width of radial plates, sloping inward, with well-developed transverse ridge, ligament pits, and other structures.

Distribution of family is in the Lower and Middle Permian of the Timor and Western Australian Permian provinces.

Affinities.—In 1949, I discussed the affinities of *Calceolispongia* and reached the conclusion that this genus could not be assigned a definite place in the system of Paleozoic crinoids. It was suggested that although the affinities were closest with *Cadocrinus*, it could not be placed in the family Cadocrinidae until the structure of the anal interradius in both genera was better known. Part of the necessary information has now been supplied by the study of *Jimbacrinus* which possesses a small, simple anal sac composed of comparatively few, relatively large plates. No known genus

of crinoids possesses an anal sac exactly like that of *Jimbacrinus*, but the Ampelocrinidae have sacs which are similar in structure, though much taller. Although in 1949 I felt "almost certain" that *Calceolispongia* possessed no anal sac, I now believe that such a structure may have been present and that it may have been similar to the anal sac of *Jimbacrinus*. This belief is based solely on the great similarity in the shape and position of the large anal plate, now interpreted as radianal, in the two genera. Failure to find traces of a calcareous tegmen in any of the numerous cups of *Jimbacrinus bostocki* is most likely due to lack of preservation of this feature.

In addition to the peculiar anal sac the following may be listed as the outstanding features of the family: rigid adherence to a fixed structure pattern of the dorsal cup and absence of any variation in plate arrangement in the anal interradius; abnormal variability in regard to shape and size of certain types of plates, especially basals; uniserial, atomous arms.

Although the origin of the family is doubtful, it seems now certain that they are a specialized, yet in some respects simplified, end branch of the suborder *Dendrocrinoidea*, as redefined by Moore and Laudon in 1943.

Genus JIMBACRINUS Teichert, n. gen.

Type species.—*Jimbacrinus bostocki* Teichert, n. sp.

Diagnosis.—Dorsal cup large, characterized by spinose basal plates, each plate bearing one or more spines which are directed outward and ventrally. Five infrabasals, subquadrangular, and partly visible in side view of cup. Radials alike, shorter than basals, weakly tuberculate.

One large anal plate present in anal interradius, supporting a short anal sac composed of comparatively large symmetrically arranged plates.

Facets of cup plates with transverse ridges. Ventral facets of radial plates identical in all essentials with those of *Calceolispongia*.

Arms atomous, uniserial; first and second brachials large, trapezoidal, tuberculate; second brachial shorter than first brachial. Second brachial followed by a row of cuneiform, pinnulate ossicles, gradually diminishing in width to the distal end of the arm.

Tegmen unknown. Stem small compared to the size of the cup; composed of alternating long and short columnals. No cirri.

The affinities of the genus with *Calceolispongia* will be discussed following the description of the type species.

JIMBACRINUS BOSTOCKI Teichert, n. sp.
Plate 13, figures 1–7
Plate 14, figures 1–11

About 60 complete cups and crowns in various states of preservation, some with stem attached, and many dissociated cup plates, columnals and brachials were available for study. There is a certain amount of variation in the size and shape of the basal plates and in the ornamentation of some of the other plates but the general pattern of cup structure is always adhered to and there is no variation in the relative position of the plates, not even in the anal region. The species is a large one, though not as large as some advanced species of *Calceolispongia*, and mature specimens, complete with stem and arms must have stood 40 to 50 cm. high.

The dorsal cup consists of 16 plates—five infrabasals, five basals, five radials and one anal plate. Above this lowest anal plate is a short anal sac and the radial plates carry long uniserial pinnulate arms. The stem is long, cylindrical and slender. In the holotype (plate 13, figs. 5–7) the diameter of the cup, not including the spines of the basal plates, is 34 mm.; its ventral lumen about 27 mm. and its length 26 mm. Some specimens are larger than the holotype, but are generally somewhat crushed and their dimensions can only be estimated. It is, however fairly certain that older individuals attain a maximum cup diameter of at least 48 mm., with a ventral lumen of about 44 mm. and a length of about 48 mm. If placed on a plane surface the cup rests on the convex central parts of the infrabasals, only a small central depression of the base of the cup being present to which the stem is attached.

There are always five infrabasal plates. These are convex both in longitudinal and in lateral cross-section, so that, in addition to the small depression in the base of the cup, shallow and narrow furrows are formed where adjoining plates meet. At least one

half of the infrabasals is visible in side view of the cup. The plates are almost rectangular in outline; in the holotype they are 10–12 mm. wide and long, but may grow to 14 or 15 mm. in larger individuals.

The basal plates are the largest plates of the cup. Seen from the inside they are roughly hexagonal, except for the posterior basal which has seven facets. Their outer side is greatly swollen and produced into one or more spines which are directed upward at an angle of approximately 45° to the longitudinal axis of the cup. In the holotype the basal plates are 17–18 mm. long and 15–17 mm. wide, and about 7–8 mm. thick. In larger cups the basals may be twice as thick and they may reach a length of 25 mm. and a width of 23 mm. In lateral view a basal plate is asymmetrical, with the greatest swelling nearer the upper (ventral) side. From this region the oblique spine (or spines) arise. In the holotype the basals carry between one and three spines and this seems to be the norm. However, there is a certain amount of variability here, because basal plates with as many as eight or nine spines or tubercles are known (plate 14, figs. 8, 9). One of the principal spines may be forked (plate 13, fig. 4). In the holotype the spines are about 4 mm. long and 3–4 mm. wide at their base, but in large specimens the spines may be up to 6 mm. long and the total distance from base of plate to tip of spine (or spines) may be as much as 20 mm. The facets of the basal plates are about 1 to 1.5 mm. wide and are incised by closely spaced transverse furrows.

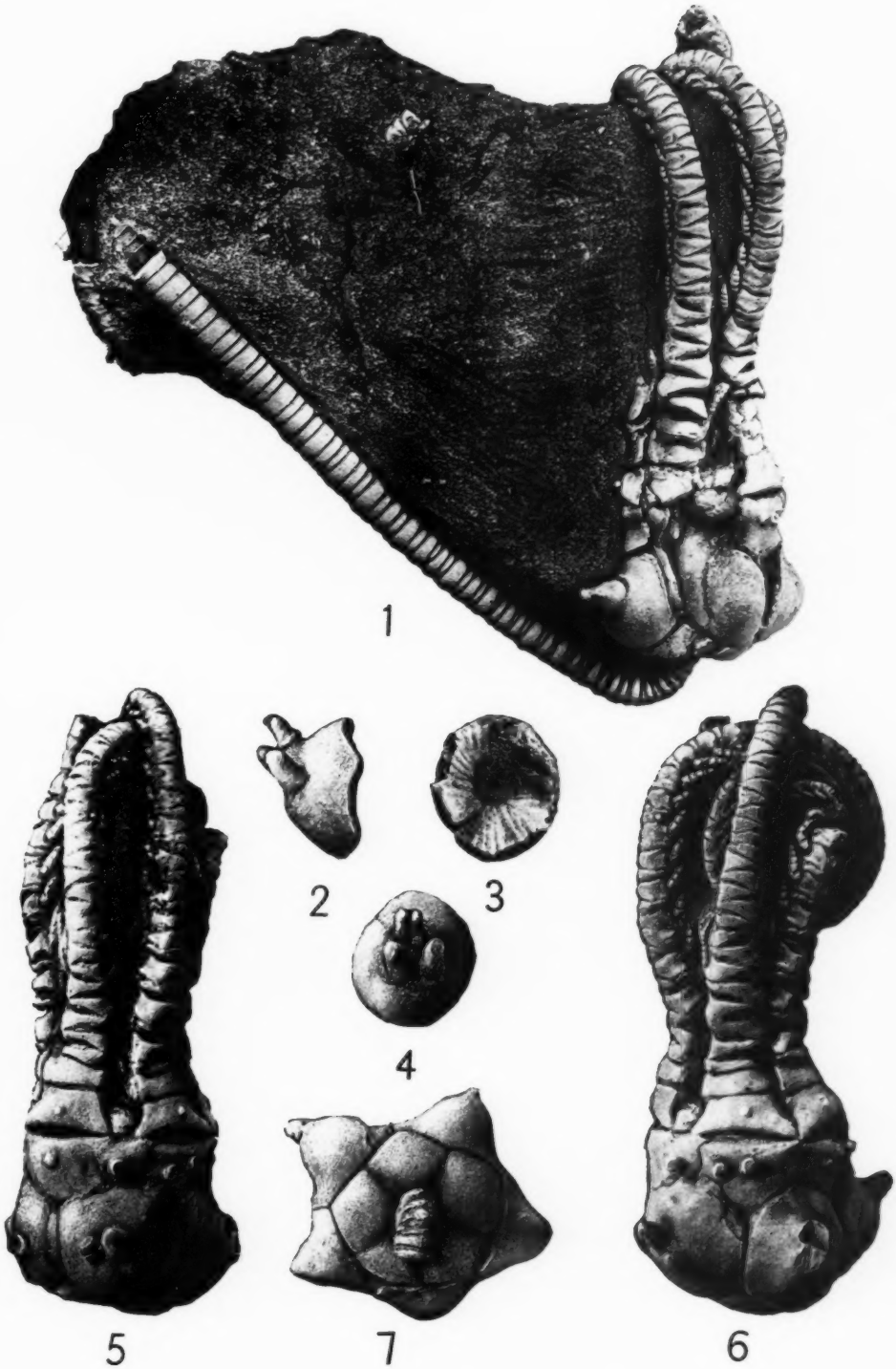
The inner side of the plates shows a system of radiating ridges (plate 13, fig. 3) which are oriented in the same way as the canal system in *Calceolispongia* (Teichert, 1949, p. 15). In this genus too the site of the canals is sometimes indicated by low internal ridges. The canals of *Calceolispongia* have been discussed in detail and it has been demonstrated that they represent part of the nervous system of that crinoid. It seems certain that *Jimbacrinus* has a similar, or identical nervous system.

The radial plates are pentagonal in outline, their greatest width being along the outside of the ventral facet. In the holotype this varies between 14 and 16 mm. In larger specimens the radials may be as much as 20 mm. wide. Their length is 10–11 mm. in the holotype, up to 13 mm. in larger individuals. The surface of most radials bears one or more prominent tubercles. Most commonly found is either one tubercle slightly above the centre of the plate, or three tubercles, with the two additional tubercles placed symmetrically on either side of the one above the centre. However, a less symmetrical arrangement is occasionally found, but the number of tubercles never seems to exceed four. Very rarely the tubercles are produced into spines which in one case are as much as 5 mm. long (plate 14, figs. 2–4). Except for these tubercles or spines the surface of the radials is only weakly convex.

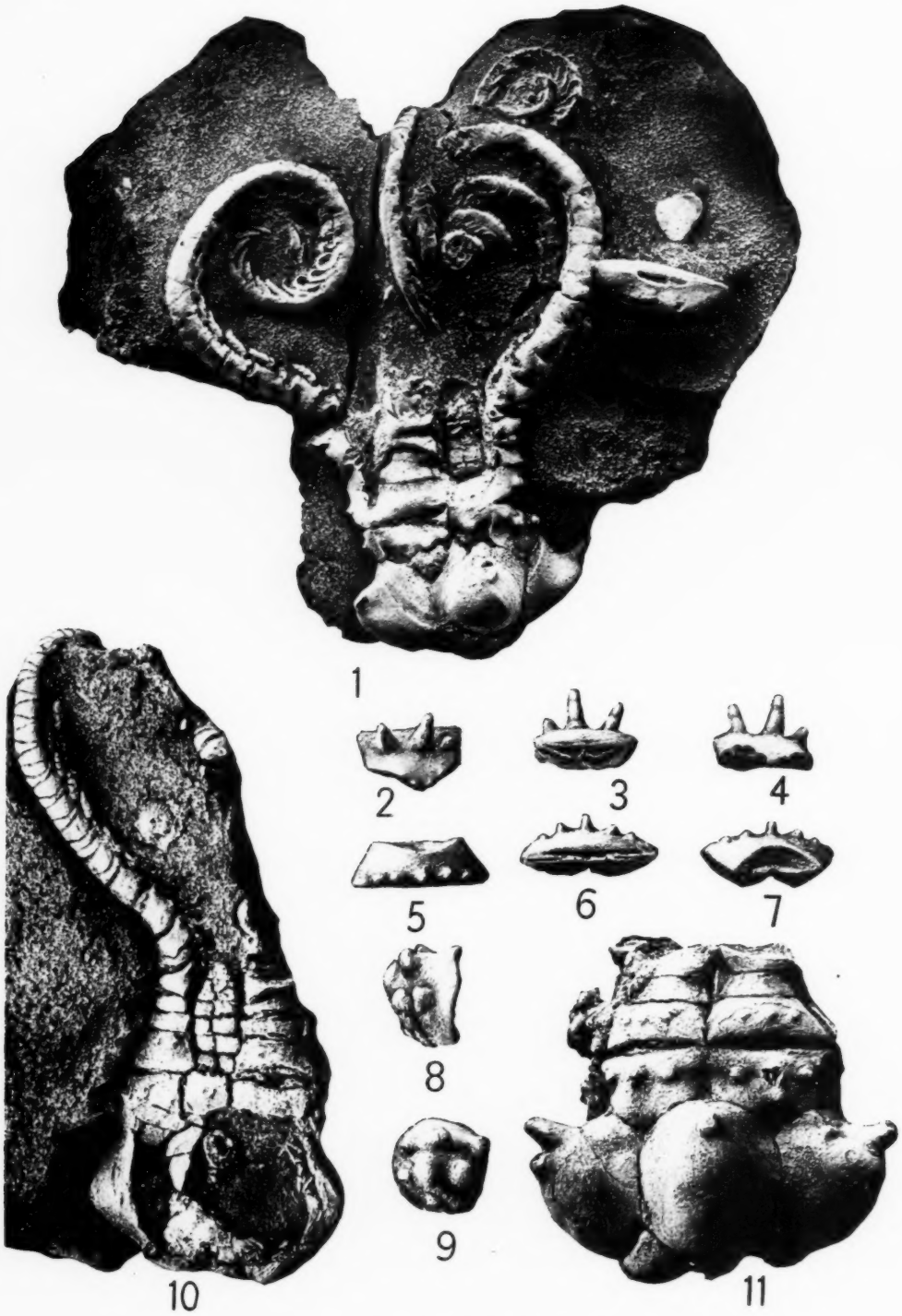
The greatest thickness of the radials is across the ventral facets. Their width seems to equal about half the length of the plate and they slope inward at an angle of 20°–30°. The outline of the ventral facet is trapezoidal with the inner margin somewhat shorter than the outer one. The morphology of this facet is almost identical with that described by me for *Calceolispongia* (Teichert, 1949, p. 11, plate 1, figs. 12, 13). A detailed comparison is not practicable because there are only few radials of *Jimbacrinus* with well preserved ventral facets available. Transverse ridge, ligament pit, outer and inner ligament area, oblique ridges, central pit, the striated muscular areas, the intermuscular ridge and the intermuscular notch are all clearly discernible. The only possible differences from conditions in *Calceolispongia* may be the absence of crenulation in the transverse ridge and of clearly defined muscular ridges, but it is not known if these features are present in all species of *Calceolispongia*. Also the internal marginal ridge of the ventral facet seems to be lower than in *Calceolispongia*. The lateral facets of the radials are roughly

EXPLANATION OF PLATE 13

FIGS. *1–7*—*Jimbacrinus bostocki* Teichert, n. sp. *1*, Paratype, complete crown with stem (no. 327); *2–4*, Lateral, interior and exterior view of irregularly spinose basal plate (no. 331); *5–7*, Holotype, viewed from anal, postero-lateral, and dorsal sides (no. 326). (p. 71)



Teichert, Australian Permian *Jimbacrinus*



Teichert, Australian Permian *Jimbacrinus*

triangular and slightly excavated in the centre. The dorsal facets are much narrower than the ventral facet. They are generally concave in cross-section and the concavity is traversed by a number of ridges whose crests are level with margins of the facets.

In the anal interradius there is one subquadrangular to compressed rectangular plate whose length equals that of the lateral facets of the two radial plates between which it lies. Its width is either equal to or somewhat smaller than its length. On its ventral side it has two separate small facets which lie in straight line and are level with the ventral facets of the radial plates. In most cups this plate is adorned with one central, more or less prominent tubercle, but one or two additional tubercles may occur. This plate corresponds to what was simply called "the anal plate" in *Calceolispongia*. I now believe that, by analogy with the more variable *Cadocrinus*, it represents most probably the radianal which has become fixed in an interradial position.

Attached to the radianal is a short anal sac the external side of which can be seen in a paratype (plate 14, fig. 10). The arrangement of the plates in the sac is highly symmetrical. Facing the outside, two rows of seven small rectangular plates, gradually diminishing in size, are placed above the two ventral facets of the radianal. In this specimen the entire anal sac above the radianal is 15 mm. long and its width in the lower half is 6 mm. Several other specimens in which the anal sac is less well preserved exhibit similar features.

Attached to the radials are uniserial arms which are sometimes rolled up and thus fully preserved. One of the arms of the holotype is thus found to be nearly 25 cm. long. The first and second brachials are different from the others and must be discussed separately.

The first brachials are trapezoidal in outline. Their surface is smooth and only slightly convex, except for one or two centrally situated tubercles which are usually not very prominent. In the holotype the first brachials are between 5.5 and 6.0 mm. long. Their width at the proximal end is equal to that of the radial facets to which they are attached, and the width at the distal end is between 10 and 12 mm., the two plates next to the anal interradius being the narrowest. Even in larger individuals the length of the first brachials does not exceed 6 mm., although the plates do, of course, become somewhat wider. Also, in old individuals they may become more tuberculate and occasionally a tubercle may grow into a short spine.

The dorsal facet of the first brachial corresponds in every respect to that of *Calceolispongia* (Teichert, 1949, p. 12, pl. 1, figs. 14, 15). The ventral facet is an elongated, shallow depression in which no further features are discernible.

The second brachials are rather featureless, nearly rectangular plates. In the holotype they are 10 to 11.5 mm. wide and uniformly 4 mm. long, and even in larger individuals the measurements lie very close to these figures. Their surface is smooth and almost straight in longitudinal section. They appear to be unornamented even in large individuals.

Beyond the second brachials follows, in each radius, a uniserial row of cuneiform plates, arranged so that successive plates point with their thin ends alternately in opposite directions. These plates diminish very gradually in width and become more broadly wedge shaped. At least from the third cuneiform plate onward pinnules appear, one pinnule being attached to the broad side of each plate. Individual pinnules are up to 11 mm. long and consist of a number of ossicles of circular cross-section and less than 1 mm. long.

In spite of presence of a number of suitably preserved cups no trace of a tegmen has been found.

The stem of the species is long, slender and

EXPLANATION OF PLATE 14

FIGS. *1–11*—*Jimbacrinus bostocki* Teichert, n. sp. *1*, Crown viewed from anal side, isolated first brachial plate in upper right hand side (no. 328); *2–4*, Outer, ventral, and dorsal views of excessively spinose radial plate (no. 332); *5–7*, Outer, dorsal and ventral views of a first brachial plate (no. 333); *8–9*, Lateral and outer views of irregularly tubercular basal plate (no. 334); *10*, Paratype, showing well-preserved anal sac (no. 329); *11*, Large cup, with some brachials (no. 330). (p. 71)

cylindrical. Characteristically, in many specimens it is sharply bent just below the cup and placed in a position pointing upward at an angle of up to 45° with the longitudinal axis of the cup. It is believed that this attitude is due to muscular contraction at the death of the animals. Generally speaking, the stem consists of alternating longer and shorter columnals, although this is not invariably so and there is no great constancy in the length of each type. In paratype no. 331 (plate 13, fig. 1) the length of the larger columnals varies between 2.5 and 1 mm., that of the smaller ones between 1.3 and 0.5 mm. The length of both types of columnals tends to decrease as the base of the cup is approached. The diameter of the stem of this particular specimen is 6 mm. Generally the figure seems to lie between 5 and 6 mm. There are no cirri.

Occurrence.—In Permian sandstones on the south side of the Gascoyne River, 2 miles east of Jimba Jimba Homestead. The Homestead is situated 95 miles upstream from the mouth of the Gascoyne River at Carnarvon. Approximate geographical coordinates of the locality are 115° 10′ E. long. and 25° 01′ S. lat. The geology of this area has not yet been studied in detail, but it seems certain that the rocks belong to the upper part of the Permian sequence as developed in the Northwest Basin. The beds should be of Artinskian age.

The crinoids occur in fossiliferous pockets in the sandstone and the cups and crowns are as a rule but little distorted. This indicates rapid sedimentation which led to quick burial of the animals, in much the same way in which this has been described for some occurrences of *Calceolispongia* (Teichert, 1949, p. 29).

Repository.—Holotype no. 326, paratypes nos. 327, 329, hypotypes nos. 328, 330–334, as well as additional specimens, numbered F.17,586, all in the collections of the Bureau of Mineral Resources, Geology, and Geophysics, Canberra.

Affinities.—In regard to the size and general structure of the crown *Jimbacrinus* resembles *Calceolispongia*, but the differences shown at the bottom of this page may be noted.

In comparing these features it should be remembered that the stem, the arms and certain cup plates of some species of *Calceolispongia* are not known. However, as far as can be stated at present stem and infrabasals of the two genera should always be easily distinguishable. The basal plates of *Jimbacrinus* are somewhat like those of *Calceolispongia spinosa* Teichert. The latter species has, however, second brachials which are typical of those of *Calceolispongia*. Also, the basal plates of *C. spinosa* never bear less than two spines, whereas many basal plates of *Jimbacrinus bostocki* have only one tubercle or spine. In fact, the basal plates of *Jimbacrinus* are most similar to plates from the Umaria beds of India, first described as fish scales by Reed and later doubtfully referred to *Calceolispongia* (Teichert 1949, p. 6).

The radials of *Jimbacrinus bostocki* are rather like those of *Calceolispongia rotundata* Teichert which differ from the known radial plates of all other species of that genus in the absence of a median depression or furrow. The ventral facets of the radial plates in both genera are, however, identical in all essential features.

The first brachials of *Jimbacrinus bostocki* are rather like those in a number of species of *Calceolispongia* and, if found iso-

	Jimbacrinus	*Calceolispongia*
Stem	Without cirri. Long and short columnals alternating fairly regularly.	With cirri. Irregular succession of longer and shorter columnals.
Infrabasals	Wide, rectangular, distinctly convex.	Lozenge-shaped and concave.
Basals	Spinose, with spines pointing about 45° upward. Limited variability.	Much bulkier plates, spines and excrescences generally pointing downward. Unlimited variability.
Radials	No median furrow present.	Median furrow generally present.
Radianal	Ventral facets level with ventral facets of adjoining radials.	Projecting beyond ventral margin of adjoining radials.
Second Brachials	Shorter than first brachials; surface smooth or weakly tuberculate.	Longer than first brachials; very bulky and strongly spinose.

lated, could hardly be distinguished. The second brachials, on the other hand, are most distinctive and in their small size and simplicity quite unlike those in any known species of *Calceolispongia*.

Jimbacrinus lacks the two or three disc-shaped ossicles which follow the second brachials in *Calceolispongia*. Beyond the second brachials the arms of *Jimbacrinus* are identical with the arms above the disc-shaped fourth or fifth brachials in *Calceolispongia abundans* and *C. multiformis*, the only two species of the genus in which the arms are known.

It will be seen that, while in respect to certain plates, *Jimbacrinus* shares the features of one or the other of the known species of *Calceolispongia*, the two genera are easily distinguished and that, more particularly, the infrabasal and the second brachial plates in them are utterly distinct.

The nervous system of the plates of the dorsal cup seems to be identical in both genera.

MANUSCRIPT RECEIVED DEC. 9, 1952

REFERENCES

MOORE, R. C., and LAUDON, L. R., 1943, Evolution and classification of Paleozoic crinoids: Geol. Soc. America, Spec. Pap., 46, 167 pp., 14 pls.

TEICHERT, C., 1949. Permian crinoid *Calceolispongia*: Geol. Soc. America, Mem. 34, 132 pp., 26 pls.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 76–78, 4 TEXT FIGS., PL. 15, JANUARY 1954

APPLICATION OF CELLULOSE PEEL TECHNIQUE TO FENESTRATE SECTIONS

JOHN W. KOENIG
Phillips Petroleum Company, Bartlesville, Oklahoma

INTRODUCTION

THE peel technique herein described was developed during a course of studies on the fenestrate Bryozoa of the Chouteau limestone formation of central Missouri. Fairly good results were obtained with the method and I feel that it may prove of value to other workers who are confronted with the problem of sectioning undulating bryozoan forms.

The technique was designed primarily for the study of the internal structure of the family Fenestrellinidae, but with variations and refinement it could be applied with equal success to any of the bifoliate or ramose forms of Bryozoa. The main problem which is encountered with any of these forms is their general undulatory character. Ordinary methods of grinding thin sections of such forms yield plane surfaces and therefore are applicable to only limited portions of the form. The peel method was devised as a solution to this difficulty in that fairly complete sections can be made of an entire form despite its undulatory character.

PREPARATION OF THE SPECIMEN

The specimen selected for study is usually fragmentary and crowded together with several other fossil remains, all of which are weathered out in varying relief upon the surface of the rock. The specimen also may be partly covered with matrix as it bends beneath the weathered surface, but other portions may stand out in complete relief. Therefore, the first step in the application of the peel technique is to trim away as much of the excess rock material as is deemed necessary for convenient handling of the specimen. The specimen should have approximately an inch or inch and one-half margin of rock surrounding it and approximately one quarter of an inch of rock beneath it (see fig. 1).

The next step is to clean the specimen thoroughly by washing and scraping away excess matrix for the purpose of exposing the frond as well as possible.

After the specimen has been cleaned, it should be placed face up in a shallow cardboard box. A Plaster of Paris mixture is then poured into the box so that the rock is completely embedded. The surface of the rock should be barely beneath the surface of the plaster. Just before the plaster hardens, while it is still tacky, the general area of the specimen can be lightly touched with a finger to roughen the plaster sufficiently for easy location of the specimen after the plaster has set.

The plaster should be permitted to harden completely by setting it in a warm, dry place overnight.

After the plaster has hardened, the cardboard box may be removed and the plaster overlying the specimen carefully scraped away with a knife blade or any other suitable scraping tool. The scraping should just expose the topmost surface of the specimen and the surrounding area of plaster should be smoothed off. The purpose of smoothing the area surrounding the specimen is to provide as even a surface as possible upon which the peel solution will rest. This provides for easy removal of the peel later on.

After the plaster shavings are cleaned away and the entire surface carefully brushed with a sable-hair brush, the specimen is ready for grinding.

GRINDING PROCEDURE

Apparatus.—The tools and materials necessary for grinding the specimen are as

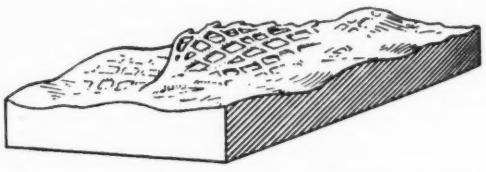


FIG. 1—A rock sample with specimen, trimmed for convenient handling.

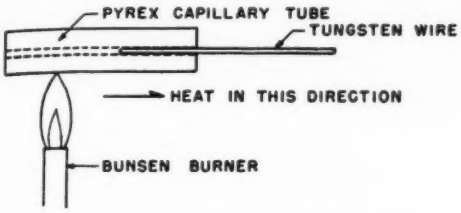


FIG. 2—Method of welding tungsten wire to pyrex glass.

follows:

1. Portable dental drill with rheostat attachment
2. Set of pyrex grinding "buttons"
3. Fine pumice
4. Light-weight mineral oil
5. Xylene
6. Half-inch flat sable brush

The portable dental drill is used to supply the rotary action of the grinding "button" and the foot control rheostat attachment regulates the rotary speed of the drill.

The pyrex grinding "buttons" are items which cannot be obtained ready-made, but they can be manufactured easily by anyone possessing the proper equipment. A short piece of tungsten wire of approximately two inches in length and of the same or slightly smaller gauge as a drill bit that will fit the chuck of the portable dental drill is welded into a small portion of pyrex glass. This is done by cleaning the tarnish from one end of the tungsten wire by heating over a Bunsen burner to white heat, then quickly running the hot wire through sodium nitrite powder.

The clean end of the wire is then inserted about half an inch into a capillary tube of pyrex glass and is welded to the glass by heating the glass in the direction of the wire (see fig. 2). This is to eliminate any air bubbles from the glass. While the glass is still soft, it should be shaped into a ball with an asbestos paddle. If the wire is properly cleaned and welded to the glass, the inserted portion of the wire will be a bright orange color upon cooling. This is a test for a properly firm union between the glass and the wire.

For shaping the grinding surface of the "button," a steel cup is used in conjunction with an ordinary drill press or the dental

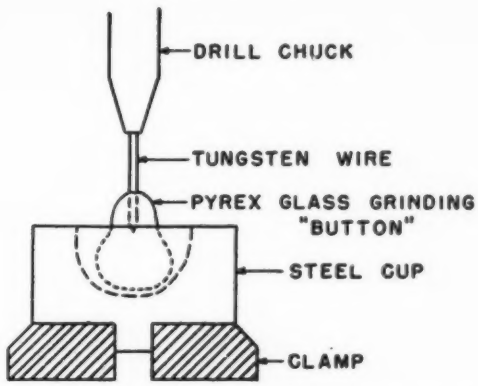


FIG. 3—Method of grinding pyrex glass "button" to desired convexity.

drill. The free end of the wire is tightened in the drill chuck and the glass ball inserted into the cup (see fig. 3). A little carborundum powder and water is then poured into the cup and the button ground to desired convexity. Figure 4 shows a typical grinding button which can be made in various sizes depending upon the work required.

Pyrex glass and tungsten wire have been specified because ordinary glass will not form a firm union with tungsten wire or steel wire. Also, pyrex glass will not form a firm union with steel wire.

This procedure was developed by Mr. Logan, the glass blower for the Department of Chemistry, University of Kansas, Lawrence.

Varying grades of grinding powder can be used depending on the requirements of the operator and the material of the speci-

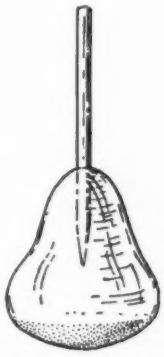


FIG. 4—A typical pyrex glass grinding "button."

men. Generally, various grades of fine-grained pumice are suitable for bryozoans which are composed of calcite. Grade numbers 600 and 1200 of pumice have been used with much success.

The fluid grinding medium of a light-weight oil was chosen because it does not soften the plaster in which the specimen is mounted. Any commercial type of mineral oil designed for household uses and small machines is satisfactory.

The xylene is used as a solvent and washing medium. This was chosen because it does not have a softening effect on the plaster.

Procedure.—The specimen is ground first by dusting a small amount of pumice on it and adding a few drops of oil. The oil and pumice are mixed together with the tip of a finger. The mixture should be a little pasty, otherwise the centrifugal force of the rotating grinding "button" will throw off the mixture and the specimen will be dry-ground. Dry-grinding should be avoided because the friction of the "button" has a tendency to pull and tear the specimen.

The grinding "button," which should be rotating at a relatively low speed, is then gently applied to the specimen.

It will be found that the plaster will absorb the oil rather quickly and that the oil-pumice mixture will become dry and stiff. At this point the specimen should be washed with a brush application of xylene. Clean oil is then dropped on the specimen and the grinding process checked under the microscope. If further grinding is necessary the above procedure is repeated until a satisfactory section is obtained.

ETCHING AND PEEL APPLICATION

Materials.—The materials necessary for etching the specimen and applying the peel solution are as follows:

1. Dilute hydrochloric acid
2. Peel solution
3. Medicine dropper
4. Half-inch flat sable brush

The strength of the dilute hydrochloric acid used should be about 3%, the proportion being 5 cc. of hydrochloric acid to 175 cc. of distilled water.

The peel solution consists of the following:

28 grams	—Paralodion
250 cc.	—Butyl Acetate
30 cc.	—Fusel Oil (Amylic alcohol)
10 cc.	—Xylene
3 cc.	—Ether
3 cc.	—Castor Oil

The medicine dropper is used for transferring the peel solution to the specimen.

Procedure.—After the specimen has been ground, it should be thoroughly cleaned with xylene and allowed to dry.

The acid is then brushed over the specimen and allowed to etch for approximately a minute or a minute and one-half, then quickly washed with water.

The specimen should dry for an hour or so before the peel solution is applied.

A relatively generous quantity of peel solution is then dropped over the specimen. The solution tends to shrink considerably upon hardening so it is advisable to inspect the peel an hour or so after application in order to see that the film will be of sufficient thickness for safe removal after it has hardened completely. This inspection is especially necessary in working with the undulatory growth forms of Bryozoa, because the solution tends to drain off the high areas. If such thinning is noticed, an additional amount of peel solution can be applied. By this time the solution surrounding the high areas is sufficiently set so that it will keep the additional solution from draining too much.

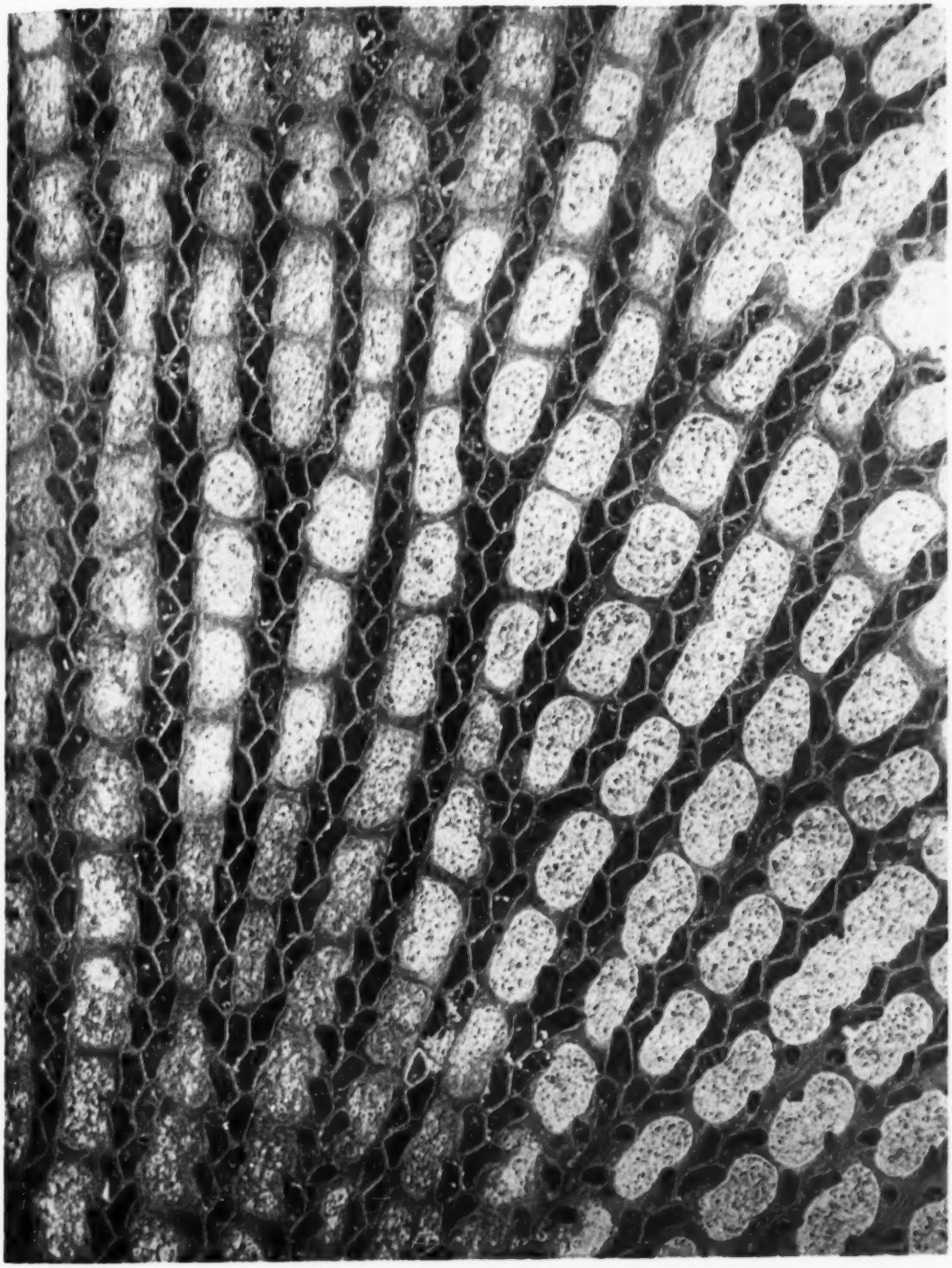
The specimen is then placed in as nearly a horizontal position as possible and allowed to stand for about 10 hours.

After the peel solution has hardened, the film can be lifted off the specimen with a knife or razor blade. The superfluous film is then trimmed away and the peel mounted and bound between two glass slides.

The peel can then be used as a photographic negative for reproduction by placing it in a photographic enlarger and projecting the image on to sensitized photographic paper of high contrast quality. Plate 15 is a representative print obtained by this procedure.

EXPLANATION OF PLATE 15

A print obtained from a cellulose peel section of the medial area of a fenestrate frond. ×28.



Koenig, peel technique for fenestrate Bryozoa

Peabody, salamander trackways

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 79–83, PL. 16, JANUARY 1954

TRACKWAYS OF AN AMBYSTOMID SALAMANDER FROM THE PALEOCENE OF MONTANA

FRANK E. PEABODY
University of Kansas, Lawrence

ABSTRACT—Trackways of a Paleocene amphibian first described by Charles W. Gilmore of the United States National Museum and referred to a Permian genus, *Ammobatrachus*, are here redescribed and placed in a new genus, *Ambystomichnus*, reflecting the affinity of the Paleocene specimens with trackways of living ambystomid salamanders, especially *Dicamptodon*.

INTRODUCTION

IN 1928 Charles W. Gilmore described several excellent trackways of an amphibian from the Paleocene Fort Union beds of Bear Butte, Montana. All the trackways are from one surface. The trackways were compared only with much older kinds from the Permian and were referred to *Ammobatrachus* Gilmore from the Coconino sandstone of Permian age in the Grand Canyon of Arizona. Gilmore (1928B) concluded that these trackways suggest "amphibian lineage," but might possibly be chelonian in origin. In the absence of amphibian bones from the Paleocene, Gilmore apparently decided not to consider the Urodela as the originator of the trackways. My own studies of Recent and Pliocene trackways of urodeles (Peabody, 1940) convince me that Gilmore's specimens are of urodelian, in particular of ambystomid origin, and should be given separate taxonomic status. Since coming to this conclusion I have learned that bones of undescribed urodeles, and salientians as well, are known from the Fort Union beds (Edward H. Taylor, personal communication).

In the present paper I attempt to redescribe Gilmore's excellent trackways and point out characteristics which indicate that these trackways represent the earliest ichnological record of the Urodela and may represent the earliest record of any kind for the urodele family Ambystomidae. Basis for the discussion is afforded by considerable data accumulated from a study of the trackways and locomotion of amphibians (Peabody, 1940, 1948) and supplemented by morphological studies of Schaeffer (1941) and Evans (1946).

EXPLANATION OF PLATE 16

Footprints of ambystomid salamanders from the Paleocene and Pliocene, and of living ambystomid, salamandrid and plethodontid salamanders (arrows indicate lateral digits).

FIG. *A*. Portion of plate 2 from Gilmore, 1928B, showing distinctly bilobate palm of the four-toed manus and drag marks of digits of *Ambystomichnus*.

B. Pes from plate 1 of Gilmore, 1928B, showing strong impression of median portion of foot

C. Clearly impressed pes from plate 3 of Gilmore, 1928B.

D–E. Two sets of manus and pes impressions of one individual of a Pliocene ambystomid (Univ. Calif. Mus. Paleo. no. 36417).

F–G. Post-mortem impressions of manus and pes, respectively, of *Dicamptodon ensatus*.

H–I. Manus and pes impressions, respectively, from the trackway (U.C.M.P. no. 36762) of the individual represented in *F–G;* trackway was recorded in sticky marl rather than sandy matrix as in *A–E*.

J. Post-mortem impressions of manus and pes of a large individual of *Dicamptodon ensatus* (Univ. Calif. Mus. Vert. Zool. no. 8573), showing bilobate palm, and tendency of decurved digit tips to make a ball-shaped impression.

K. Sample from trackway (U.C.M.P. no. 36745) of *Triturus torosus*, a short-coupled salamandrid, which usually leaves a tail mark.

L. Sample from trackway (U.C.M.P. no. 36768) of *Ensatina eschscholtzii*, a short-coupled plethodontid, which often leaves no tail mark because the tail is regularly carried off the ground. *A–C*, ×½; *D–L*, ×1.

Dr. David Dunkle of the United States National Museum has kindly supplied a photograph and a plaster duplicate of the trackways shown by Gilmore (1928B, plates 1 and 2). Drs. Henry H. Lane and Edwin C. Galbreath gave the manuscript a helpful, critical reading.

SYSTEMATIC DESCRIPTION

Family AMBYSTOMIDAE

Genus AMBYSTOMICHNUS Peabody, n. gen.

Type species.—*Ambystomichnus montanensis* (Gilmore) = *Ammobatrachus montanensis* Gilmore 1928B.

Material.—USNM no. 7635; casts of trackways from one surface, preserved upon separate slabs.

Horizon and locality.—Paleocene of Bear Butte, Montana; Bear Butte Pass, Sweetgrass County, Section 8, T. 5 N., R. 16 E.

Diagnosis.—Trackways of a large urodele amphibian indicating an individual comparable in body form with the living ambystomid genus *Dicamptodon*, the marbled salamander, but twice as large and slightly longer in the trunk region. Details of the footprints agree closely with footprints of living and Pliocene ambystomids, and the bilobate palm of the manus is exactly as in the living *Dicamptodon ensatus*. Stride 18 cm. maximum; pace angulation (defined below) 77 degrees maximum; manus 3.1 cm. wide, pes 3.7 cm. wide overall; both relatively distant from midline.

DISCUSSION

There are several points in Gilmore's description which necessitate comment before presenting the thesis of the present paper. The trackway designated as typical by Gilmore (1928B, pl. 1) has irregularities in the gross pattern related to an abrupt change of direction. As the tetrapod turned to one side (left), the left manus was turned inward more than usual; the right manus was pointed forward in normal position. Thus, the in-turned print of the left manus is not a specific character, as Gilmore states, but reflects only a change in direction of body movement. As shown in Gilmore's plates 2 and 3, each manus is directed forward in regular fashion when the tetrapod walked a straight line; and the longitudinal axis of the trackway parallels digit III of the manus.

In the trackways shown in Gilmore's plates 2 and 3, impressions of the right and left pes tend to point to the right; and in plate 2, the impressions of the manus are displaced to the right side. These peculiarities have no taxonomic value. A sidling motion of a primitive tetrapod climbing obliquely a gentle to steep incline results in a "toeing up" so that all four feet tend to point upslope for better purchase; and the pattern of manus impressions may track to one side or the other relative to the pattern of pes impressions even though the amphibian be walking on level ground. These nonspecific habits are plainly shown in trackways of living and Pliocene salamanders and also in the many excellent trackways of *Laoporus* from Permian rocks of the Grand Canyon.

Gilmore's diagram (1928B, fig. 1) is incorrect in that the first footprint on the left side is drawn as a manus but is actually a pes, and the second footprint on the same side is drawn as a pes, but is actually a manus. This artifact adds to the apparent peculiarities of the type specimen.

Gilmore's caption "natural size" for pl. 3 indicates a much smaller size for this figured trackway than for the trackways shown in pls. 1 and 2 where "$\frac{1}{3}$ natural size" is indicated. It is suspected that the caption of pl. 3 should also read "$\frac{1}{3}$ natural size" since the written description does not indicate a size difference of this magnitude.

The Paleocene footprints are relatively widely spaced from each other and from the midline—much more so than for the Permian *Ammobatrachus* in which the footprints are relatively large and close to the midline. Also the ratio of pes length to stride is much higher (1 to 5) than for *Ammobatrachus* (1 to 2). Consecutive imprints of the hind feet determine a series of angles, using the base of digit III as the apex of consecutive, alternating, acute angles (pace angulation) which average 67, 63, and 77 degrees in the Paleocene trackways shown in pls. 1, 2, and 3, respectively. These values compare favorably with those for living and Pliocene ambystomids, and are consistently higher than for the Permian *Ammobatrachus* with 62 degrees pace angu-

lation. The only important similarity between the Paleocene and Permian trackways is that both show 4 toes on the manus and 5 on the pes; but many Permian amphibians and most urodeles have this characteristic. Also, palm and sole differ in shape, and the Permian form lacks offset outer digits.

Lastly, and quite apart from the above observations, it does not seem advisable to refer evidences of Paleocene vertebrates to Permian species even though the similarity be much greater than is the case here. The paleontological record of the Urodela, although far from complete, indicates a long history for the group and a remarkable stability of genera during the Cenozoic era. The genera *Triturus* and *Salamandra* are known from the Miocene, and *Plioambystoma*, nearly identical with *Ambystoma*, is known from the Pliocene. Also, trackways of *Triturus*, *?Dicamptodon* and *Batrachoseps* have been identified from the lower Pliocene (Peabody, 1940), a clear indication that three families of terrestrial salamanders—the Salamandridae, Plethodontidae and Ambystomidae—were as well differentiated at the beginning of Pliocene time as they are now. Under the circumstances it seems much more likely that the amphibian trackways described by Gilmore (1928B) have affinities with a Cenozoic amphibian rather than with any Paleozoic form. This supposition is entirely justified because the Paleocene trackways appear completely familiar to one acquainted with trackways of living salamanders, particularly the ambystomid, *Dicamptodon*.

Comparison of the Paleocene footprints with selected Recent and Pliocene ambystomid footprints of comparable degree of impression is effectively done by placing them together in plate 16. Disregarding differences of size, the similarity of the best footprints from the Paleocene, Pliocene and Recent becomes marked to the point of identity, especially so as concerns the Paleocene and Pliocene specimens. In the manus, characters are the same and, of particular interest, the palm is bilobate with the inner lobe most pronounced, characters found in living salamanders only in *Dicamptodon*, the giant marbled salamander. In the clearest impressions of the pes the similarity is again most striking between Paleocene and Pliocene specimens. The outer digits are slightly longer than in *Dicamptodon* but no longer than in *Ambystoma gracile*. Selected impressions (figs. B, E, I) show the tendency toward indistinct impression of the outer digit of the pes and a correspondingly strong impression of the inner side of the pes—a basic amphibian character but peculiar to ambystomids among living terrestrial urodeles.

The Paleocene footprints show a relatively long first digit on manus and pes, and among terrestrial salamanders the ambystomids alone have this characteristic. In salamandrids of western North America and Asia the inner and outer digits are more or less equal in length, but short, even nubbin-like. If they are long, as in European forms, they are still noticeably shorter than the much longer digits II, III and IV. In plethodontids the inner digit of the pes is nubbin-like as is also the inner digit of the manus. Finally, only the ambystomids show a noticeable and consistant offset of the outer digit of manus and pes. Ambystomids when walking tend to point digit III of the manus forward so that it parallels the longitudinal axis of the trackway; in salamandrids the longitudinal axis usually passes between digits II and III of the manus; in plethodontids it coincides with digit III, but the manus is functionally tridactyl, digit I being very small and nubbin-like.

The footprints shown in plate 16 exhibit a variable degree of bulbosity at the blunt digit tips. A bulbous digit tip is frequently seen in urodele trackways (Peabody, 1948, pl. 28), but it is also common in trackways of Paleozoic amphibians. Study of Recent urodeles (Peabody, 1940) has shown that the digit tip impression is not a reliable indication of the shape of the digit tip itself. For example, footprints F and G in plate 16 are post-mortem and were obtained by pressing the foot of a dead *Dicamptodon* into clay and casting the impression in plaster. These impressions show no pronounced bulbosity yet the trackway impression of this individual when alive (H–I) seems to indicate bulbous digit tips. By contrast, *Aneides lugubris*, a plethodontid, shows bulbous digit tips in its trackway (Peabody,

1948, pl. 28) and it actually has expanded digit tips. Thus, impressions of a seemingly bulbous digit tip seen in amphibian trackways are more an expression of amphibian locomotion in which the supple foot is "rolled" forward in the walking movement, and the digit tip depressed or flexed for better purchase.

Antero-posterior spacing of the manus relative to the pes indicates that the Paleocene ambystomid had a relatively longer dorsal region than *Dicamptodon* and most other ambystomids except *Rhyacotriton*. In two trackways (Gilmore, 1928, pl. 1, 3) the manus regularly occurs midway between consecutive pedes on one side, and in the third trackway (pl. 2) it is forward of a point halfway between pedes. Judging from the more or less similar mode of impression of all three trackways it seems probable that the third trackway represents a different individual and one with a somewhat longer dorsal region. A specimen of *Dicamptodon* in which the dorsal region is 5 cm. long and the extended front and hind limb (including extended feet) are 2.9 and 3.6 cm. long overall, respectively, placed the manus regularly just in front of the pes and noticeably less than halfway between pedes or about $\frac{1}{3}$ the distance. A long-bodied ambystomid, *Rhyacotriton*, in which the dorsal region is 3.3 cm. and the limbs are 1.1 and 1.3 cm. long, respectively, placed the manus regularly well forward of half way between pedes or about $\frac{2}{3}$ the distance. Thus, the length of the dorsal region relative to the length of the limbs in the Paleocene ambystomid was somewhere between the proportions indicated for *Dicamptodon* and *Rhyacotriton*. The Paleocene ambystomid was approximately 20 cm. long in the dorsal region as judged from trackway dimensions, therefore, approximately 50 cm. long overall.

The Paleocene trackways represent an ambystomid of somewhat larger size than any known from living faunas. *Dicamptodon*, a monotypic genus, and the largest of living ambystomids, may reach a length of at least 30 cm. The largest individual for which a trackway has been recorded is 17 cm. long and is of average size for the species (*D. ensatus*). Its dorsal region (glenoid-acetabular distance) is 5 cm. long. This animal had an average stride of 6 cm. A large individual 30 cm. long overall would probably nearly double this stride and therefore would approach the stride of *Ambystomichnus*, which varies between 13.5 and 18 cm.

The footprints of a *Dicamptodon* of medium size are approximately $\frac{1}{3}$, of a large individual $\frac{2}{3}$, as large as *Ambystomichnus*. In my opinion the greater size of the Paleocene footprints in no way bars them from consideration as ambystomid in origin. Rather, the view is taken that Paleocene ambystomids as well as later representatives may have been larger than any living today. The large size of the body indicated by the Paleocene footprints is not excessive and falls within the range reasonable for amphibians of the urodele type, albeit near the maximum range for terrestrial urodeles of ambystomid form.

Width of footprint across outer digit tips

Dicamptodon ensatus	manus	pes
Pl. 16 F, G,	1.3 cm	1.7
*U.C.M.V.Z. 8573	1.8	2.2
Pliocene ambystomid †(U.C.M.P. 36417)	1.6	2.0
Paleocene ambystomid	3.1	3.7

* Univ. Calif. Mus. Vert. Zool.
† Univ. Calif. Mus. Paleo.

The Paleocene trackways are typically urodelian in several secondary characteristics: the frequent but erratic occurrence of long drag-marks made by digit tips; some of the drag-marks lead to the footprint as well as away from it, and may impart a bifurcate appearance to the tip of the digit (Gilmore, 1928B, pl. 3); drag-marks made by the manus and pes differ in that those made by the manus describe a simple, lateral curve, whereas those made by the pes describe first a short reverse curve before entering on a long lateral curve (Peabody, 1948, fig. 11); lastly, the absence of a definite and regular tail mark, contrary to one's expectation for heavy-tailed tetrapods, is characteristic of most ambystomid and plethodontid (fig. L) trackways, and this is true of the Paleocene trackways. The Paleocene ambystomid undoubtedly possessed a tail like that of *Dicamptodon*, that is, one rounded in cross section, at least in that part which dragged most heavily on the recording surface.

CONCLUSIONS

The Paleocene trackways, *Ambystomichnus montanensis* (Gilmore), are comparable to those recorded by *Dicamptodon ensatus* but differ in the wider spacing of manus and pes antero-posteriorly, and in having slightly longer lateral digits on manus and pes. Comparable length of digits is found in *Ambystoma gracile*. The manus of *Ambystomichnus* shows a bilobate palm identical with that of *Dicamptodon* which is unique among living ambystomids in that character. In all general characteristics except size *Ambystomichnus* is comparable with the trackways of living terrestrial salamanders. Ambystomid trackways from the Pliocene of California show foot characters identical with the Paleocene specimens except for smaller size, and these, although belonging to a short-bodied form comparable to *Dicamptodon*, serve as a connecting link in an ichnological history of the Ambystomidae.

The Paleocene trackways are most similar to those of living ambystomids which inhabit heavily forested regions especially characterized by conifers among which redwoods are common. The Paleocene Fort Union flora indicates a well-forested region in which redwoods (*Metasequoia*) were fairly common (Chaney, 1951). Thus, there is the interesting environmental association of giant, *Dicamptodon*-like salamanders with a redwood forest assemblage during Paleocene times in Montana.

MANUSCRIPT RECEIVED JULY 29, 1952

LITERATURE CITED

CHANEY, R. W., 1951, A revision of fossil *Sequoia* and *Taxodium* in Western North America based on the recent discovery of *Metasequoia:* Trans. Amer. Phil. Soc. (N.S.), 40, 171–239, 12 pls.

EVANS, F. G., 1946, The anatomy and function of the foreleg in salamander locomotion: Anatomical Rec., 95, 257–281, 6 figs.

GILMORE, C. W., 1928A, Fossil footprints from the Grand Canyon: Third contribution: Smithsonian Misc. Collect., 80, no. 8, 16 pp., 7 figs., 5 pls.

——, 1928B, Fossil footprints from the Fort Union (Paleocene) of Montana: Proc. U. S. Nat. Mus., 74, no. 5, 4 pp., 1 fig., 3 pls.

PEABODY, F. E., 1940, Trackways of Pliocene and Recent salamandroids of the Pacific Coast of North America: (Thesis for degree of M.A., Univ. Calif., 1940).

——, 1948, Reptile and amphibian trackways from the Lower Triassic Moenkopi formation of Arizona and Utah: Univ. Calif. Publ., Bull. Dept. Geol. Sci., 27, 295–468, 40 figs., 22 pls.

SCHAEFFER, BOBB, 1941, The morphological and functional evolution of the tarsus in amphibians and reptiles: Bull. Amer. Mus. Nat. Hist., 78, 395–472, 21 figs.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 84–95, 3 TEXT FIGS., JANUARY 1954

DISTRIBUTION OF AMERICAN PENNSYLVANIAN CEPHALOPODS

A. G. UNKLESBAY
University of Missouri, Columbia, Missouri

ABSTRACT—Cephalopods are locally abundant in Pennsylvanian marine sediments, particularly in Texas and Oklahoma, and in much of the northern Mid-Continent. Ammonoids are particularly valuable in zonation and correlation of the strata in which they are preserved. There has been reported and well documented the occurrence of 110 species comprising 36 genera. A total of 25 nautiloid genera has been reported but the species are not diagnostic of age.

INTRODUCTION

CEPHALOPODS are locally abundant in Pennsylvanian marine sediments. The strata of Texas and Oklahoma have yielded the greatest abundance of material, and except in Iowa and central Missouri, those of the northern Mid-Continent region have also been rather prolific. Relatively small numbers of cephalopods have been reported from the Pennsylvanian beds of the Appalachian region, or from those of the Illinois and Michigan basins.

The ammonoids, because of their several well-established evolutionary trends, which can be rather easily observed, are useful in zonation and correlation of the strata in which they are preserved. The nautiloids, because of having less well-defined evolutionary trends are less useful for stratigraphic purposes, although a few genera are rather restricted in range.

The accompanying charts show the range of well-documented occurrences of 36 ammonoid genera, 110 ammonoid species, and 25 nautiloid genera. The nautiloid species do not seem diagnostic enough to warrant charting. The occurrences recorded on the charts are largely from the publications of A. K. Miller and his associates, and of Plummer and Scott. Also, I have had access to two unpublished manuscripts by Miller, and by Miller and Furnish, for which I am duly grateful. The work of other authors has also been used where well documented. The numbers above the range-lines in the ammonoid species chart refer to the bibliographic reference in which the species is said to occur at the position indicated.

Several genera of cephalopods survived the close of the Mississippian period and ranged into the Pennsylvanian. The stocks which survived were rather diverse and gave rise to still more diverse groups out of which rose the large number and variety of ammonoids and nautiloids which characterize many Permian sediments. Although the phylogenetic relationships of the Pennsylvanian forms are not too well understood at the present time, some tentative suggestions concerning the ammonoids are indicated on the chart showing ranges of ammonoid genera.

DISTRIBUTION OF AMMONOIDS

Springeran.—Despite the fact that several ammonoid genera survived the Mississippian only one species *Pseudoparalegoceras friscoense* Miller and Owen is known to occur in beds of Springeran age. All the known representatives of this species are from the lower part of the Springer formation in Pontotoc County, Oklahoma.

Zone of Gastrioceras.—The ammonoids of the zone of *Gastrioceras* are known largely from their occurrence in the Hale sandstone and Bloyd shale of Arkansas and Oklahoma, and in the Union Valley sandstone of the Arbuckle-Ouachita region of Oklahoma. A few have also been reported from the Dornick Hills formation, the Wesley shale, and the Round Prairie sandstone.

Altogether these Morrowan beds have yielded the following ammonoid species:

Anthracoceras sp.
Pronorites arkansasensis Smith
Cravenoceras? morrowense Miller and Moore
Bistoceras secundum Miller and Moore
Gastrioceras adaense Miller and Owen
Gastrioceras branneri Smith
Gastrioceras fittsi Miller and Owen
Gastrioceras grileyi Miller and Owen
Eoasianites oblatus Miller and Moore
Pseudoparalegoceras kesslerense (Mather)

Zone of Paralegoceras.—The most prolific formations in this zone are the Atoka

of Oklahoma, the Smithwick and its equivalents in Texas, and the "Winslow" formation of Arkansas.

The Marble Falls limestone of north-central Texas has yielded the following species:

Eoasianites raymondi (Plummer and Scott)
Pronorites llanoensis Plummer and Scott
Pseudoparalegoceras compressum (Hyatt)
Paralegoceras texanum (Shumard)

A zone about fifty feet below the top of the Smithwick in north-central Texas has yielded the following:

Gastrioceras occidentale (Miller and Faber)
G. smithwickense Plummer and Scott
G. listeri (Martin)
G. branneri Smith
Nuculoceras smithwickense Plummer and Scott
Diaboloceras varicostatum Miller and Furnish
Pseudoparalegoceras lenticulare (Plummer and Scott)
Pseudoparalegoceras bellilineatum Miller and Furnish
Boesites scotti (Miller and Furnish) [=*Paraprolecanites sandbergeri* Plummer and Scott]
Pronorites arkansasensis Smith
Eoasianites raymondi (Plummer and Scott)
Proshumardites primus Plummer and Scott

Near the north end of the Sierra Diablo mountains a shale of Smithwick age has yielded the following:

Boesites scotti (Miller and Furnish) = *Paraprolecanites sandbergeri* Plummer and Scott
Eoasianites raymondi (Plummer and Scott)
Pseudoparalegoceras lenticulare (Plummer and Scott)
Gastrioceras smithwickense Plummer and Scott
Gastrioceras occidentale (Miller and Faber)
Proshumardites primus Plummer and Scott

In the Atoka and equivalent beds in Oklahoma the following fauna has been found:

Agathiceras sp.
Pronorites siebenthali Smith
Bisatoceras sp.
Gastrioceras cf. *G. listeri* (Martin)
Eoasianites sp.
Pseudoparalegoceras williamsi Miller and Downs
Paralegoceras iowense (Meek and Worthen)
P. texanum (Shumard)
Diaboloceras varicostatum Miller and Furnish

The "Winslow" formation of western Arkansas has yielded *Pseudoparalegoceras williamsi* Miller and Downs and *Winslowoceras henbesti* Miller and Downs.

The lower Cherokee of Iowa has yielded *Paralegoceras iowense* (Meek and Worthen) and *Wiedeyoceras sanctijohanis* (Wiedey). Whether the beds which contained these two forms are part of the Cherokee proper, or belong in the Atokan is not clearly understood.

Zone of Owenoceras—This zone is represented in the Mid-Continent region, in north-central Texas, and in the Appalachian region.

The following forms have been found in the Kickapoo Falls limestone of north-central Texas.

Pseudoparalegoceras brazoense Plummer and Scott
Eoasianites welleri (Smith)
Owenoceras hyattianus (Girty)

The Boggy formation of Oklahoma has produced:

Anthracoceras oklahomense Miller and Owen
Pseudoparalegoceras brazoense Plummer and Scott
Eoasianites sp.

Anthracoceras wanlessi Plummer and Scott has been reported from the limestone above the No. 2 coal in Illinois.

The Cherokee of west-central Missouri has been the most prolific unit in this zone and has been found to contain the following:

Imitoceras cherokeense Miller and Owen
Dimorphoceras politum (Shumard)
Bisatoceras greeni Miller and Owen
Goniloboceras eliasi Miller and Owen
Eoasianites welleri (Smith)
E. moorei (Miller and Owen)
Owenoceras bellilineatum (Miller and Owen)
Anthracoceras wanlessi Plummer and Scott

In eastern Ohio the Vanport and Hamden beds of the Alleghenyan series has produced the following:

Gonioglyphioceras sp.
Eoasianites cf. *E. globulosus* (Meek and Worthen)
Neoshumardites sp.
Wellerites sp.

Although these beds in Ohio and Pennsylvania are usually correlated with other beds of the lower part of the Desmoinesian the fauna might well be considered as typical of the zone of *Wellerites*.

Zone of Wellerites—The Wewoka, Wetumka, and Holdenville formations of east-central Oklahoma have yielded a rather large and varied ammonoid fauna which contains the following species:

Boesites girtyi Plummer and Scott
Neodimorphoceras oklahomae (Girty)
Bisatoceras sp.
Gonioglyphioceras gracile (Girty)
Eudissoceras venatum (Girty)
Agathiceras sp.
Eoasianites angulatum (Girty)
E. excelsum (Meek)
Owenoceras hyattianum (Girty)
Peritrochia sp.
Wellerites sp.

A fauna very similar to this also occurs in the Buckhorn asphalt in south-central Oklahoma.

Anthracoceras wanlessi Plummer and Scott is also known from beds of Marmaton age in western Missouri.

In north-central Texas the base of the Mineral Wells formation contains *Pintoceras postvenatum* Plummer and Scott, *Eoasianites welleri* Smith, and a species of *Goniloboceras*. In the same area the East Mountain shale has yielded *Neodimorphoceras lenticulare* (Girty), *Goniloboceras bridgeportense* Plummer and Scott, *Owenoceras hyattianum* (Girty) and *Schistoceras hildrethi* (Morton).

Zone of Eothalassoceras.—The fauna of this zone has a rather limited vertical extent and seems to be characteristic of the basal parts of the Missourian series near Collinsville, Oklahoma. Here the Seminole formation has yielded the following:

Eothalassoceras inexpectans (Miller and Owen)
Bisatoceras primum Miller and Owen
Eudissoceras collinsvillense Miller and Owen
Eoasianites clinei (Miller and Owen)
E. jonesi (Miller and Owen)
E.? prone (Miller and Owen)
Owenoceras retiferum (Miller and Owen)
Schistoceras hildrethi (Morton)

The Coffeyville formation, which is slightly younger than the Seminole contains a few of the same species and is also reported to yield *Eoasianites kansasensis* (Miller and Gurley). *Schistoceras missouriense* (Miller and Faber) is known from the lower part of the Conemaugh in Ohio and the bed in which it was found may belong to this zone.

Zone of Prouddenites.—In this zone there occurs a rather varied group of ammonoids typified by those from the Nellie Bly and Ochelata beds of Oklahoma. There are:

Prouddenites primus Miller
Boesites texanus (Böse)
Imitoceras grahamense (Plummer and Scott)
Eothalassoceras inexpectens (Miller and Owen)
Eudissoceras pingue (Miller and Cline)
Goniloboceras goniolobum (Meek)
G. gracellenae Miller and Cline
G. welleri Smith
Eupleuroceras bellulum Miller and Cline
Eoasianites millsi (Miller and Cline)
Dunbarites rectilateralis (Miller)
Schistoceras hildrethi (Morton)
Neoshumardites sp.
Parashumardites senex (Miller and Cline)
Peritrochia ganti (Smith)

Eoasianites globulosus (Meek and Worthen) is known from the Drum limestone of northeastern Oklahoma.

The Kansas City group of eastern Kansas and western Missouri lies within this zone and its various units have yielded ammonoids as follows:

Westerville limestone
Eoasianites kansasensis (Miller and Gurley)
Goniloboceras goniolobum (Meek)
Schistoceras hildrethi (Morton)
S. missouriense (Miller and Faber)
Muncie Creek shale
Prouddenites primus Miller
Eoasianites sp.
Schistoceras hildrethi (Morton)
S. missouriense (Miller and Faber)
Argentine limestone
Stenopronorites kansasensis (Newell)
Goniloboceras goniolobum (Meek)

In addition to the above listed forms a few isolated specimens have been listed from unidentified beds in the Kansas City Group. These are: *Milleroceras parrishi* (Miller and Gurley) and *Goniloboceras welleri* Smith.

The Lansing beds of eastern Kansas have yielded *Neodimorphoceras texanum* (Smith).

The Francis formation of the Arbuckle Mountains of Oklahoma has yielded poorly preserved specimens which seem to be referable to *Neodimorphoceras oklahomae?* and *Eoasianites?* sp.

Miller and Furnish (unpublished manuscript) say that "in the Mid-Continent region *Prouddenites* appears to be characteristic of the Kansas City Group."

The Graford formation of north-central Texas has yielded the following ammonoids:

Eoasianites gaptankensis (Miller)
E. anguloumbilicatus (Plummer and Scott)
E. angulatus (Girty)
Schistoceras missouriense (Miller and Faber)
S. hildrethi (Morton)
Peritrochia parkeri (Heilprin)
Prouddenites boesei (Smith)
Goniloboceras bridgeportense Plummer and Scott

Parashumardites fornicatus (Plummer and Scott)
Pronorites pseudotimorensis Miller

In the same area the Caddo Creek beds have yielded:

Eoasianites stainbrooki (Plummer and Scott)
Uddenites harlani Plummer and Scott
Trochilioceras tenuosum Plummer and Scott
Shumardites moorei Plummer and Scott
S. uddeni (Böse)

In the Marathon area of western Texas this zone is represented by *Shumardites sellardsi* Plummer and Scott and *Owenoceras hyattianum* (Girty) in the middle part of the Gaptank formation, and by a fairly large fauna reported by Plummer and Scott from a boulder of unknown stratigraphic position.

The genus *Schistoceras* is also known from the McLeansboro in central Illinois and from the lower part of the Conemaugh in eastern Ohio and western Pennsylvania. Some of the lower Conemaugh occurrences may belong in the zone of *Eothalassoceras*.

Zone of Uddenites.—The beds which lie above the Kansas City group in the northern Mid-Continent region contain relatively few ammonoids but at a few localities they are fairly abundant. The genus *Uddenites*, which characterizes the middle Cisco of Texas, has not been reported from the northern Mid-Continent region. Miller and Furnish (unpublished manuscript) report that *Schistoceras hildrethi* (Morton) occurs in the Iatan limestone of the Pedee group, and in the Haskell and Robbins members of the Douglas group. The Robbins has also yielded specimens of *Gonioloboceras* and *Eoasianites*. The Heebner shale of the Shawnee group has yielded the following genera: *Eothalassoceras*, *Eoasianites*, *Shumardites*, *Peritrochia*.

J. P. Smith (1932) reported the occurrence of *Eoasianites* and *Peritrochia* in the lower Wabaunsee near Howard, Kansas. *Imitoceras*, *Eudissoceras*, and *Goniolaboceras* are also known to occur in the Dover limestone near Piedmont, Kansas, and in the Grandhaven at Emporia. These are apparently the youngest ammonoids in the northern Mid-Continent region.

In north-central Texas the Finis shale near the base of the Graham formation has been reported to bear a rather large ammonoid fauna containing the following species:

Uddenites schucherti Böse
Eudissoceras pingue (Miller and Cline)
Eoasianites kansasensis (Miller and Gurley)
Schistoceras missouriense (Miller and Faber)
S. hildrethi (Morton)
Peritrochia ganti (Smith)
P. sulcatus (Böse)
Goniolaboceras welleri Smith
Agathiceras frechi Böse
A. ciscoense Smith
Shumardites cuyleri Plummer and Scott
Imitoceras [= *Neoaganides*] *grahamense* (Plummer and Scott)
Trochilioceras tenuosum Plummer and Scott
Eothalassoceras kingorum (Miller)
Prehoffmania milleri Plummer and Scott

Also in north-central Texas the upper part of the Graham formation has yielded the following:

Boesites texanus (Böse)
Uddenites schucherti Böse
U. serratus Plummer and Scott
Eothalassoceras caddoense (Plummer and Scott)
Eoasianites kansasense (Miller and Gurley)
E. globulosus (Meek and Worthen)
Eudissoceras pingue (Miller and Cline)
Schistoceras hildrethi (Morton)
S. missouriense (Miller and Faber)
Shumardites simmondsi Smith
Peritrochia sulcatus (Böse)
P. vidriensis (Böse)
Goniolaboceras welleri Smith
Neodimorphoceras texanum (Smith)
Agathiceras ciscoense Smith

In the vicinity of Jacksboro, Texas, the basal Graham has been reported to contain *Gastrioceras montgomeryense* Miller and Gurley, *Goniolaboceras gracellenae* Miller and Cline, *Neodimorphoceras plummerae* Plummer and Scott, and *Shumardites moorei* (Plummer and Scott). Also listed from the Graham of Brown County, Texas, is *Millerroceras parrishi*.

In the Marathon area the *Uddenites* zone is one of the best-known ammonoid zones in Texas. Here the uppermost part of the Gaptank formation in the Glass Mountains has yielded the following species:

Uddenites schucherti Böse
Eoasianites kansasensis (Miller and Gurley)
E. modestus (Böse)
E. ruzencevi Miller and Furnish
Boesites texanus (Böse)
Schistoceras missouriense (Miller and Faber)
S. hildrethi Morton
Agathiceras frechi Böse
Peritrochia vidriensis (Böse)
P. sulcatus (Böse)
P. ganti (Smith)

Shumardites uddeni (Böse)
S. irregulare (Böse)
S. simmondsi Smith
Neodimorphoceras texanum (Smith)

DISTRIBUTION OF THE NAUTILOIDS

At least 25 nautiloid genera are now known from rocks of Pennsylvanian age. Twelve of these ranged throughout the period. At least ten of the twelve were survivors of the Mississippian. Twelve genera continued from Pennsylvanian into the Permian. Seven of the twelve which ranged throughout the Pennsylvanian also ranged from Mississippian into the Permian.

Only one nautiloid is known from beds of Springeran age and it is a poorly preserved orthoconic form which is probably a species of *Pseudorthoceras*.

The Mid-Continent region of the United States has produced the greatest abundance of Pennsylvanian nautiloids, and in this region they are distributed throughout much of the Pennsylvanian section and occur in many stratigraphic units. In central Oklahoma, the Morrowan Union Valley formation has yielded a small fragment tentatively referred to *Mooreoceras* and several specimens which probably are conspecific with *Liroceras liratum* (Girty). The Boggy of the same area has yielded *Liroceras liratum* (Girty), and the Wewoka has been reported to contain the following:

Brachycycloceras crebricinctum (Girty)
B. normale Miller, Dunbar, and Condra
Euloxoceras greenei Miller, Dunbar, and Condra
Liroceras liratum (Girty)
L. obsoletum (Girty)
Mooreoceras tuba (Girty)
Pseudorthoceras knoxense (McChesney)
Pseudometacoceras sculptile (Girty)

The Atoka of Arkansas has also yielded *Ephippioceras ferratum* (Cox).

The Cherokee beds of west-central Missouri have yielded a rather large and varied fauna composed of the following:

Brachycycloceras longulum Miller and Owen
Domatoceras umbilicatum Hyatt
D. williamsi Miller and Owen
Endolobus depressus (Hyatt)
Ephippioceras ferratum (Cox)
Knightoceras missouriense Miller and Owen
Liroceras missouriense (Miller and Owen)
Megaglossoceras pristinum Miller and Owen
Metacoceras biseriatum Miller and Owen
M. mutabile Miller and Owen
Mooreoceras normale Miller, Dunbar, and Condra
Foordiceras crassum (Hyatt)
P. bellatulum Miller and Owen
Poterioceras bransoni Miller and Owen
P. mehli Miller and Owen
Pseudorthoceras knoxense (McChesney)
Solenochilus newloni (Hyatt)
S. peculiare Miller and Owen
Temnocheilus harneri Miller and Owen

The Marmaton Labette shale in eastern Missouri has yielded *Euloxoceras greenei* Miller, Dunbar, and Condra.

In the Mid-Continent area the beds of Missourian age have been more prolific over a wider area than other beds and a considerable fauna is known from these strata in Missouri, Kansas, Nebraska, northwestern Arkansas, and northern Oklahoma. The Kansas City group has been especially prolific and the following occurrences are known:

Bronson subgroup.—
Hertha limestone
Mooreoceras normale Miller, Dunbar, and Condra
Bethany Falls limestone of Iowa
Planetoceras tiltoni Miller, Dunbar, and Condra
Coffeyville formation of Oklahoma
Metacoceras vagans Miller and Owen
Liroceras reticulatum Miller and Owen
Dennis formation of eastern Kansas and western Missouri
Condraoceras primum Miller, Lane, and Unklesbay
Domatoceras kleihegei Miller, Lane, and Unklesbay
Ephippioceras ferratum (Cox)
Knightoceras abundum Miller, Lane, and Unklesbay
Liroceras milleri (Newell)
Metacoceras jacksonense Miller, Lane, and Unklesbay
M. mutabile Miller and Owen
Mooreoceras bakeri Miller, Dunbar, and Condra
M. conicum Miller, Lane, and Unklesbay
M. tuba (Girty)
Solenochilus missouriense Miller, Lane, and Unklesbay
Linn subgroup.—
Cherryvale formation of Kansas
Domatoceras toddanum (Gurley)
Ephippioceras ferratum (Cox)
Metacoceras angulatum Sayre
M. cavatiforme Hyatt
Mooreoceras normale Miller, Dunbar, and Condra
Titanoceras? ingens Miller, Dunbar, and Condra
T. rectilaterale Miller, Dunbar, and Condra

Nellie Bly formation of Oklahoma
Liroceras liratum (Girty)
Pseudorthoceras knoxense (McChesney)
Francis formation of Oklahoma
Ephippioceras ferratum (Cox)
Euloxoceras greenei Miller, Dunbar, and Condra
Drum limestone of Kansas
Domatoceras moorei Miller, Dunbar, and Condra
Zarah subgroup.—
Wyandotte formation
Kionoceras sp. (May not be *Kionoceras* s.s.)
Koninckioceras eliasi Newell
K. wyandottense Newell
Liroceras milleri Newell
Megaglossoceras rectilaterale Miller, Dunbar, and Condra
Mooreoceras bakeri Miller, Dunbar, and Condra
M. condrai Newell
Solenochilus brammeri Miller, Dunbar, and Condra

The Lansing group has yielded only a few nautiloids as follows:

Plattsburg formation
Koninckioceras jewetti Newell
Liroceras greenei Miller, Dunbar, and Condra
Metacoceras inconspicuum Hyatt
Mooreoceras condrai Newell
Stanton formation
Kionoceras sp.
Liroceras obsoletum Girty
Ephippioceras ferratum (Cox)
Mooreoceras tuba (Girty)

The Pedee group has yielded *Liroceras liratum* (Girty) from the Weston shale, and *Mooreoceras tuba* (Girty) from the Iatan limestone.

The McLeansboro of Illinois which is essentially equivalent to the Missourian series is reported to have yielded *Megaglossoceras montgomeryense* (Worthen), *Metacoceras sangamonense* (Meek and Worthen) and *Titanoceras illinoiense* (McChesney).

The Virgilian series of the Mid-Continent region has yielded a rather varied nautiloid fauna most of which came from the Shawnee group.

Oread formation of Kansas:
Dolorthoceras? dubium Miller, Dunbar and Condra
Mooreoceras bakeri Miller, Dunbar, and Condra
M. normale Miller, Dunbar, and Condra
M. tuba (Girty)
Pseudorthoceras sculptile (Girty)
Solenochilus kerefordensis Miller, Dunbar, and Condra
Tainoceras monilifer Miller, Dunbar, and Condra
T. rotundatum Miller, Dunbar, and Condra
Titanoceras ponderosum (Meek)

Only three species have been reported from the Wabaunsee group of the Mid-Continent region. The Neva limestone has produced *Metacoceras sublaeve* Miller, Dunbar, and Condra and the Burlingame limestone has yielded *Mooreoceras bakeri* Miller, Dunbar, and Condra, and *Tainoceras monilifer* Miller, Dunbar, and Condra.

In north-central Texas several nautiloids have been found in various formations. The Caddo Creek has yielded *Euloxoceras greenei* Miller, Dunbar, and Condra. The Graham formation has been the most prolific unit in Texas and its members have yielded nautiloids as follows:

Finis shale:
Brachycycloceras normale Miller, Dunbar, and Condra
Tainoceras monilifer Miller, Dunbar, and Condra
Jacksboro limestone
Euloxoceras greenei Miller, Dunbar, and Condra
Liroceras liratum (Girty)
L. obsoletum (Girty)
Mooreoceras tuba (Girty)
Wayland shale
Brachycycloceras normale Miller, Dunbar, and Condra
Pseudometacoceras sculptile (Girty)

Also in north-central Texas the Cisco has been reported to contain *Dolorthoceras ciscoense* Miller, Dunbar, and Condra and *Pseudorthoceras knoxense* (McChesney) but the particular horizon from which these species came is not known.

The Kendrick shale of Kentucky has yielded the following forms:

Brachycycloceras kentuckiense Miller, Dunbar, and Condra
Coelogasteroceras canaliculatum (Cox)
Megaglossoceras magnum Miller, Dunbar, and Condra
Mooreoceras normale Miller, Dunbar, and Condra
Planetoceras bellilineatum Miller, Dunbar, and Condra
Pseudometacoceras sculptile (Girty)
Temnocheilus subrectangularis Miller, Dunbar and Condra

In the Appalachian region the nautiloid fauna has become well known in the last few years and the Alleghenyan and Conemaughan beds have yielded quite a variety of nautiloids in eastern Ohio, and western

Pennsylvania. The producing beds and the species produced are as follows:

Alleghenyan
Vanport limestone
Domatoceras sp.
Metacoceras tricarinatum Sturgeon
Foordiceras sp.
Poterioceras curtum Meek and Worthen
P. subellipticum Miller and Unklesbay
Pseudorthoceras knoxense (McChesney)
Solenochilus bognari Sturgeon
Temnocheilus quinqueliratus Sturgeon
Hamden limestone
Brachycycloceras ohioense Sturgeon
Domatoceras obsoletum Sturgeon
D. shepherdi Sturgeon
Ephippioceras ferratum (Cox)
Liroceras liratum (Girty)
Metacoceras sp.
M. lambi Sturgeon
M. perelegans Girty
Mooreoceras normale Miller, Dunbar, and Condra
Poterioceras curtum (Meek and Worthen)
Pseudorthoceras knoxense (McChesney)
Solenochilus greenensis Sturgeon
Temnocheilus medioventralis Sturgeon
Washington shale
Domatoceras shepherdi Sturgeon
Pseudorthoceras knoxense (McChesney)
Conemaughan
Brush Creek limestone
Coelogasteroceras dubium Miller and Unklesbay
Domatoceras sp.
Ephippioceras ferratum (Cox)
Liroceras sp.
Megaglossoceras sp.
Metacoceras cornutum Girty
M. perelegans Girty
Mooreoceras normale Miller, Dunbar, and Condra
Poterioceras curtum (Meek and Worthen)
Pseudorthoceras knoxense (McChesney)
Solenochilus brammeri Miller, Dunbar, and Condra
Stenopoceras smithi Miller and Unklesbay
Pine Creek limestone
Domatoceras sp.
Megaglossoceras sp.
Metacoceras cornutum Girty
M. perelegans Girty
Pseudorthoceras knoxense (McChesney)
Solenochilus brammeri Miller, Dunbar, and Condra
Woods Run limestone
Domatoceras sp.
Ephippioceras ferratum (Cox)
Metacoceras cornutum Girty
M. perelegans Girty
Tainoceras monilifer Miller, Dunbar, and Condra
Ames limestone
Domatoceras sp.
Metacoceras cornutum Girty
M. perelegans Girty
Mooreoceras normale Miller, Dunbar, and Condra
Poterioceras curtum (Meek and Worthen)
Pseudorthoceras knoxense (McChesney)
Pseudometacoceras sculptile (Girty)
Tainoceras monilifer Miller, Dunbar, and Condra

In the Rocky Mountain area the *Stenopoceras* beds of the Casper formation in Wyoming have yielded the following forms:

Liroceras sp.
Metacoceras sp.
Metacoceras knighti Miller and Thomas
M. sulciferum Miller and Thomas
Mooreoceras sp.
Pseudorthoceras knoxense (McChesney)
Solenochilus brammeri Miller, Dunbar, and Condra
Stenopoceras abundum Miller and Thomas
Tainoceras wyomingense Miller and Thomas

The Pennsylvanian beds of the Sangre de Cristo region in Colorado have produced *Liroceras greenei* Miller, Dunbar, and Condra, *Megaglossoceras johnsoni* Miller, Dunbar, and Condra, and *Temnocheilus johnsoni* Miller, Dunbar, and Condra.

SUMMARY

The occurrence and distribution of Pennsylvanian cephalopods as now known are shown in the accompanying charts and described in this text. However, it should be mentioned that this work may present a distorted picture of the actual distribution of these forms in Pennsylvanian rocks because there are almost certainly many other occurrences that are unknown or as yet unstudied. Further work in the Rocky Mountain region and in the Sangre de Cristo will probably yield additional faunas. Also closer scrutiny of the Appalachian region and the Illinois and Michigan basins will probably produce more material. It should also be stressed that more detailed study of both the ammonoids and nautiloids is needed to aid in better understanding the phylogenetic relationships.

SELECTED REFERENCES FOR AMMONOIDS

Note: Numbers refer to numbers on ammonoid chart

1. Miller, A. K., and Owen, J. B., 1944, The cephalopod fauna of the Pennsylvanian Union Valley formation of Oklahoma: Jour.

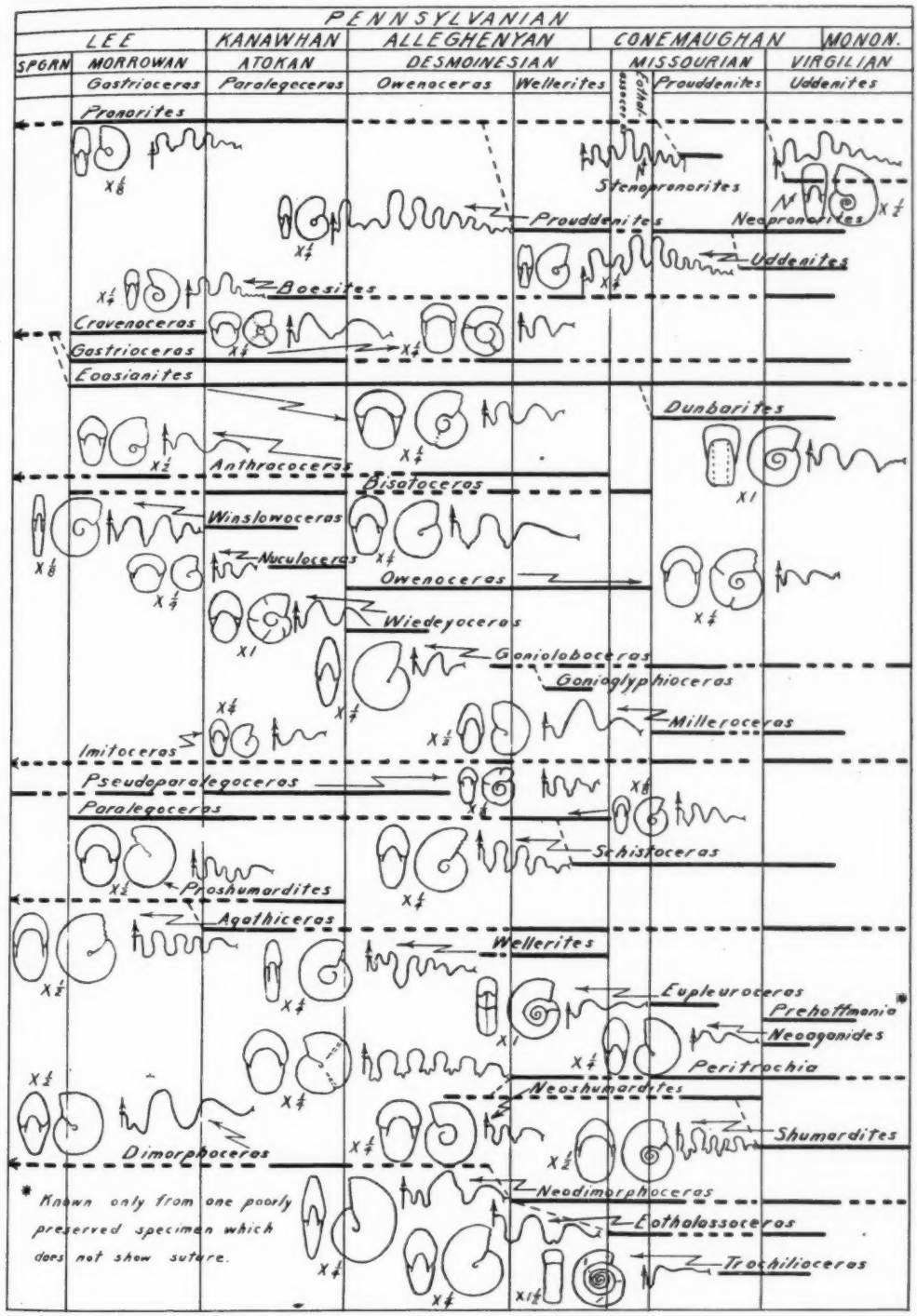
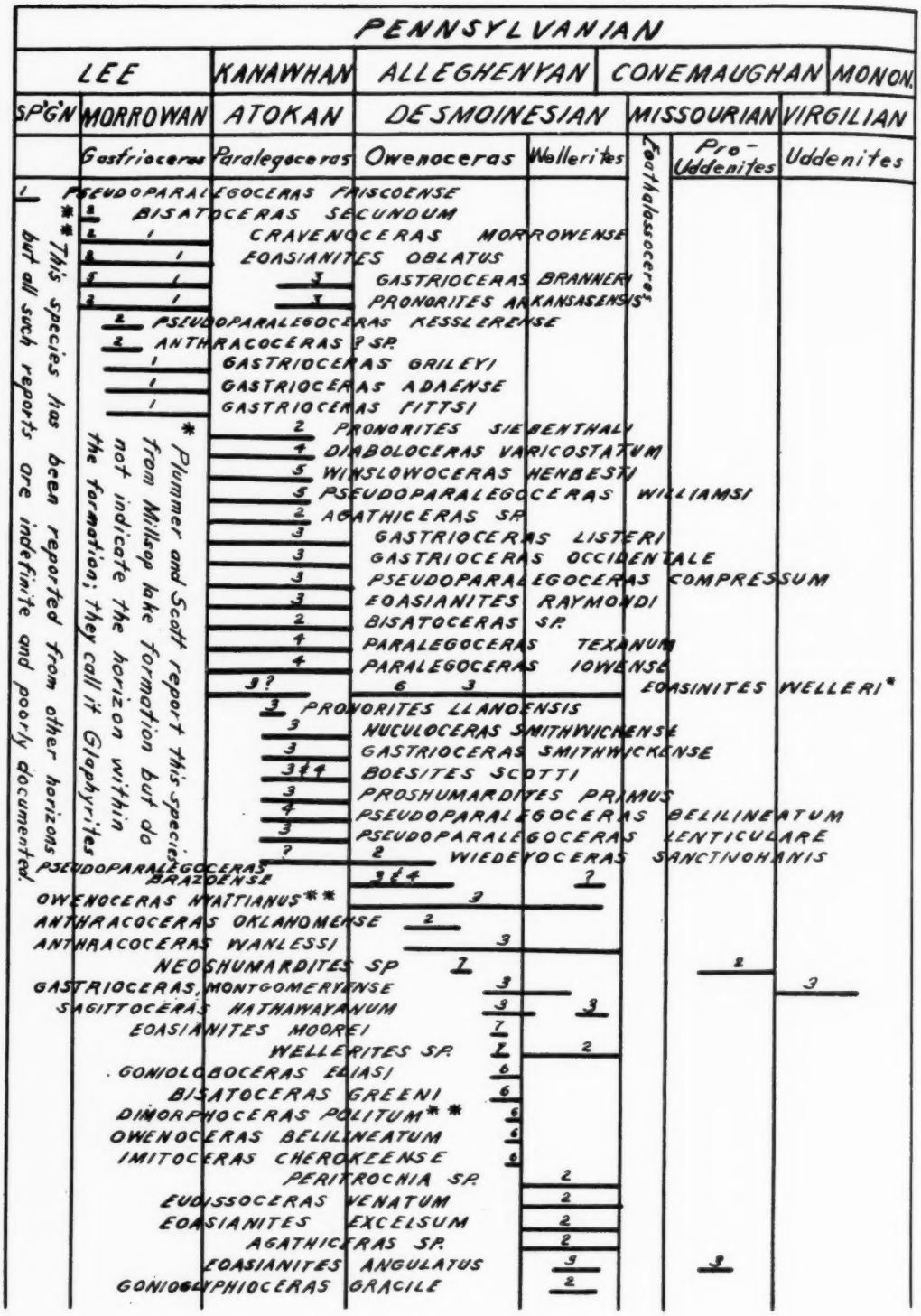


FIG. 1—Range chart of Pennsylvanian ammonoid genera.


PENNSYLVANIAN
LEE
KANAWHAN
ALLEGHENYAN
CONEMAUGHAN
MONON.
SP'GN
MORROWAN
ATOKAN
DESMOINESIAN
MISSOURIAN
VIRGILIAN
Gastrioceras
Paralegoceras
Owenoceras
Wellerites
Boathalassoceras
Pro-Uddenites
Uddenites
PSEUDOPARALEGOCERAS FAISCOENSE
BISATOCERAS SECUNDUM
CRAVENOCERAS MORROWENSE
EOASIANITES OBLATUS
GASTRIOCERAS BRANNERI
PRONORITES ARKANSASENSIS
PSEUDOPARALEGOCERAS KESSLERENSE
ANTHRACOCERAS ? SP.
GASTRIOCERAS GRILEYI
GASTRIOCERAS ADAENSE
GASTRIOCERAS FITTSI
PRONORITES SIEBENTHALI
DIABOLOCERAS VARICOSTATUM
WINSLOWOCERAS HENBESTI
PSEUDOPARALEGOCERAS WILLIAMSI
AGATHICERAS SP.
GASTRIOCERAS LISTERI
GASTRIOCERAS OCCIDENTALE
PSEUDOPARALEGOCERAS COMPRESSUM
EOASIANITES RAYMONDI
BISATOCERAS SP.
PARALEGOCERAS TEXANUM
PARALEGOCERAS IOWENSE
EOASINITES WELLERI*
PRONORITES LLANOENSIS
NUCULOCERAS SMITHWICKENSE
GASTRIOCERAS SMITHWICKENSE
BOESITES SCOTTI
PROSHUMARDITES PRIMUS
PSEUDOPARALEGOCERAS BELILINEATUM
PSEUDOPARALEGOCERAS LENTICULARE
WIEDEYOCERAS SANCTIJOHANIS
PSEUDOPARALEGOCERAS BRAZOENSE
OWENOCERAS NATTIANUS**
ANTHRACOCERAS OKLAHOMENSE
ANTHRACOCERAS WANLESSI
NEOSHUMARDITES SP
GASTRIOCERAS MONTGOMERYENSE
SAGITTOCERAS HATHAWAYANUM
EOASIANITES MOOREI
WELLERITES SP.
GONIOLOBOCERAS ELIASI
BISATOCERAS GREENI
DIMORPHOCERAS POLITUM**
OWENOCERAS BELILINEATUM
IMITOCERAS CHEROKEENSE
PERITROCHIA SP.
EUDISSOCERAS VENATUM
EOASIANITES EXCELSUM
AGATHICERAS SP.
EOASIANITES ANGULATUS
GONIOGYPHIOCERAS GRACILE
* Plummer and Scott report this species from Millsap lake formation but do not indicate the horizon within the formation; they call it Glaphyrites
** This species has been reported from other horizons but all such reports are indefinite and poorly documented.

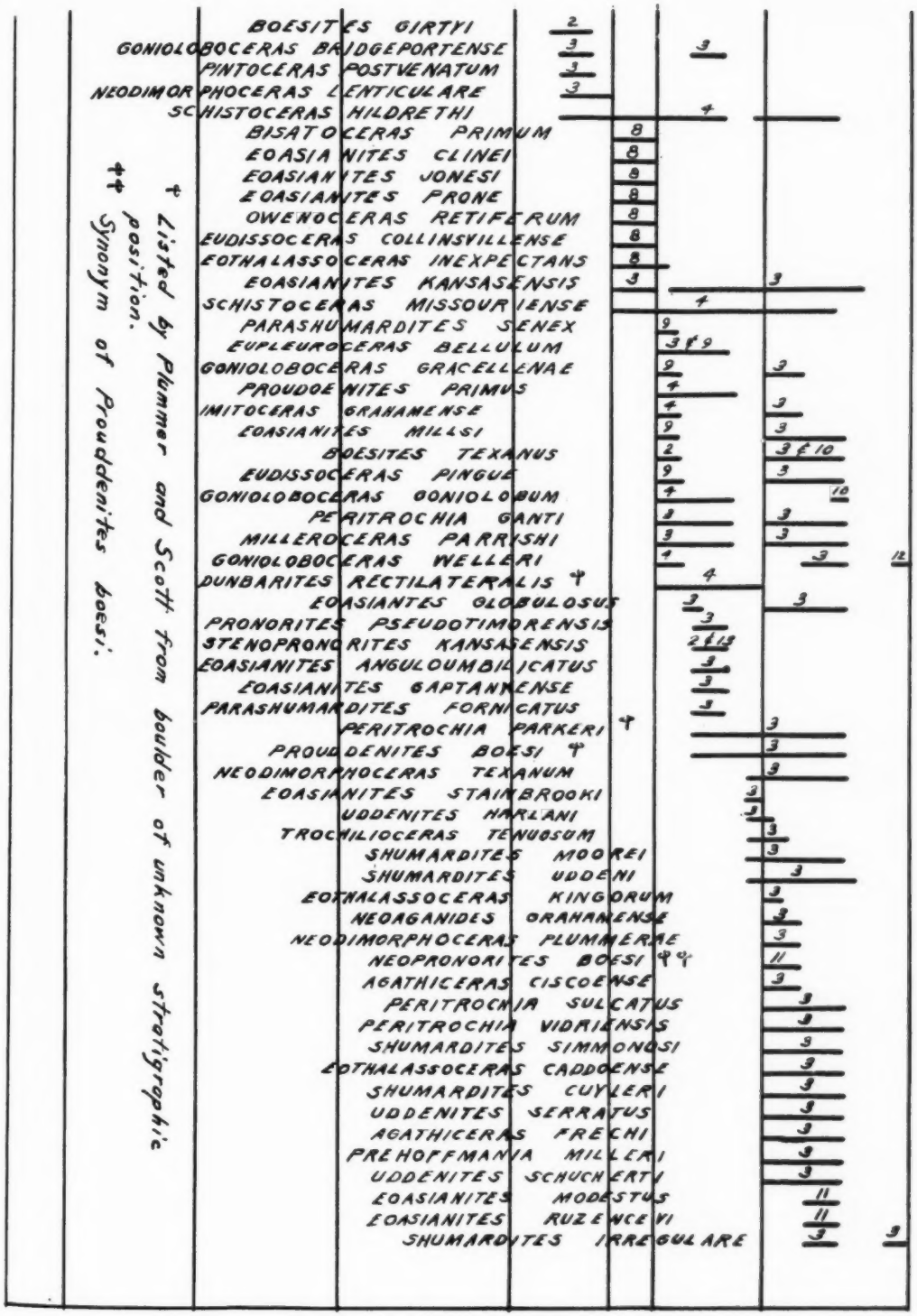
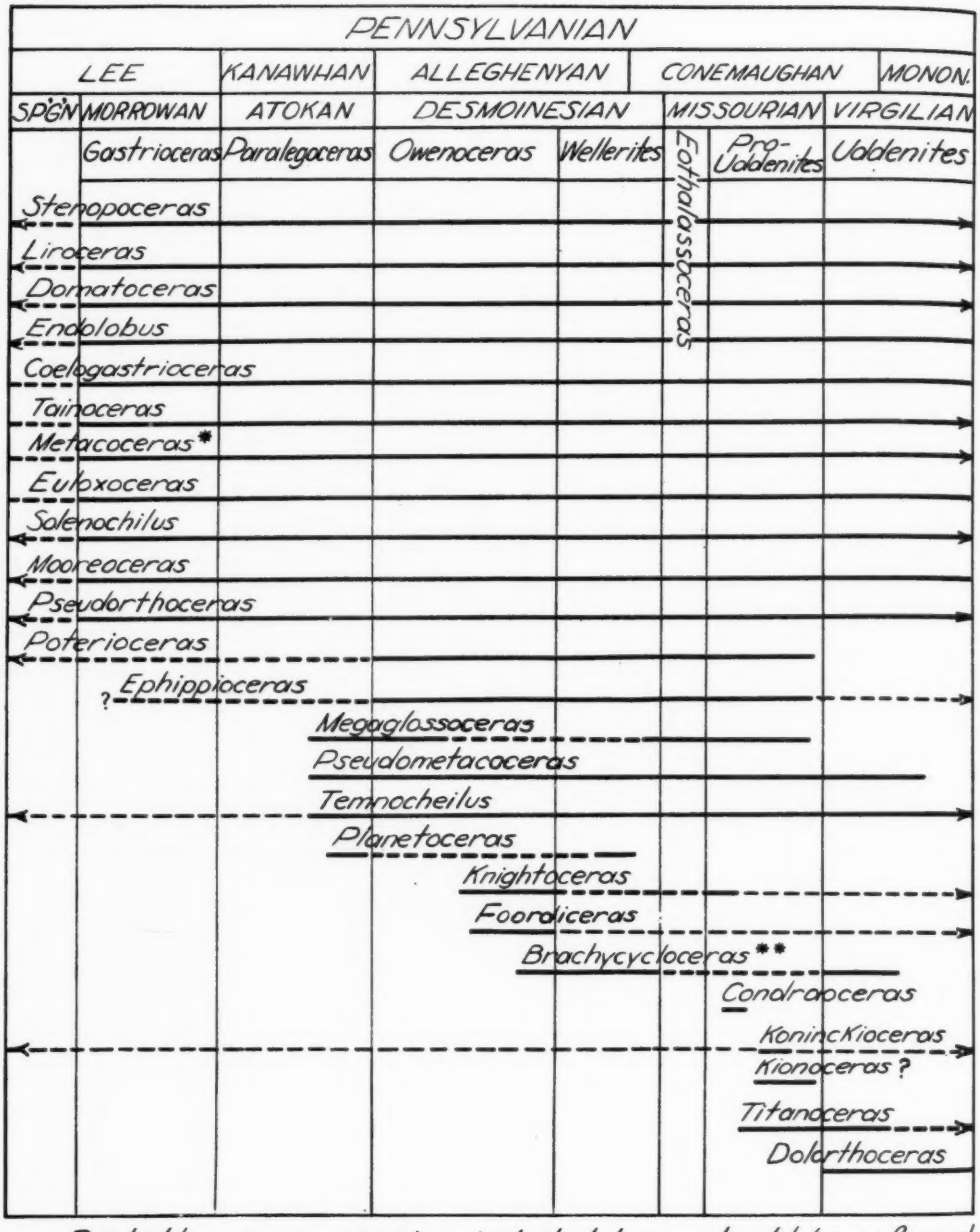


FIG. 2—Range chart of Pennsylvanian ammonoid species.



* Probably some species included here should be referred to Foordiceras.

** Known in Permian of Eastern Hemisphere.

FIG. 3—Range chart of Pennsylvanian nautiloid genera.

Paleontology, vol. 18, pp. 417–428, pls. 63–68.

2. MILLER, A. K., and FURNISH, W. M., Pennsylvanian and Permian ammonoids of the northern Mid-Continent region. Unpublished manuscript.
3. PLUMMER, F. B., and SCOTT, GAYLE, 1937, Upper Paleozoic ammonites of Texas: Texas Univ. Bull. 3701, pp. 1–516, pls. 1–41.
4. MILLER, A. K., and FURNISH, W. M., 1940, Studies of Carboniferous ammonoids: Parts 5–7: Jour. Paleontology, vol. 14, pp. 521–543, pls. 62–65.
5. ———, and DOWNS, R. H., 1948, A cephalopod fauna from the type section of the Pennsylvanian "Winslow formation" of Arkansas: Jour. Paleontology, vol. 22, pp. 672–680, pls. 101–103.
6. ———, and OWEN, J. B., 1939, An ammonoid fauna from the Lower Pennsylvanian Cherokee formation of Missouri: Jour. Paleontology, vol. 13, pp. 141–162, pls. 17–20.
7. ———, and STURGEON, M. T., 1946, Allegheny fossil invertebrates from eastern Ohio —Ammonoidea: Jour. Paleontology, vol. 20, pp. 384–389, pl. 56.
8. ———, and OWEN, J. B., 1937, A new Pennsylvanian cephalopod fauna from Oklahoma: Jour. Paleontology, vol. 11, pp. 403–422, pls. 50–52.
9. ———, and CLINE, L. M., 1934, The cephalopod fauna of the Pennsylvanian Nellie Bly formation of Oklahoma: Jour. Paleontology, vol. 8, pp. 171–185, pl. 28.
10. SHIMER, H. W., and SHROCK, R. R., 1944, Index Fossils of North America. John Wiley and Sons, New York.
11. MILLER, A. K., and FURNISH, W. M., 1940, Permian ammonoids of the Guadalupe Mountain region and adjacent areas: Geol. Soc. America, Sp. Pap. 26.
12. ELIAS, M. K., 1938, Studies of late Paleozoic ammonoids: Jour. Paleontology, vol. 12, pp. 86–105, pls. 19, 20.
13. NEWELL, N. D., 1936, Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda: Jour. Paleontology, vol. 10, p. 481–489, pls. 68–72.

MANUSCRIPT RECEIVED FEBRUARY 16, 1953

SELECTED REFERENCES FOR NAUTILOIDS

GIRTY, G. H., 1915, The fauna of the Wewoka formation of Oklahoma: U. S. Geol. Survey Bull. 544, pp. 1–353, pls. 1–35.

MILLER, A. K., and CLINE, L. M., 1934, The cephalopod fauna of the Pennsylvanian Nellie Bly formation of Oklahoma: Jour. Paleontology, vol. 8, pp. 171–185, pl. 28.

——, DUNBAR, C. O., and CONDRA, G. E., 1933, The nautiloid cephalopods of the Pennsylvanian system in the Mid-Continent region: Nebraska Geol. Survey, Bull. 9, 2nd ser., pp. 1–240, pls. 1–24.

———, LANE, J. H., JR., and UNKLESBAY, A. G., 1947, A nautiloid cephalopod fauna from the Pennsylvanian Winterset limestone of Jackson County, Missouri: Univ. Kansas, Paleont. Contr., Mollusca, Art. 2, pp. 1–11, pls. 1–5.

———, and MOORE, CARL A., 1938, Cephalopods from the Carboniferous Morrow group of northern Arkansas and Oklahoma: Jour. Paleontology, vol. 12, pp. 341–354, pls. 43, 44.

———, and OWEN, J. B., 1934, Cherokee nautiloids of the northern Mid-Continent region: Univ. Iowa, Studies Nat. Hist., vol. 16, pp. 185–272, pls. 8–19.

———, and THOMAS, H. D., 1936, The Casper formation of Wyoming and its cephalopod fauna: Jour. Paleontology, vol. 10, pp. 715–738, pls. 96–99.

———, and UNKLESBAY, A. G., 1942, The cephalopod fauna of the Conemaugh series in western Pennsylvania: Carnegie Museum Annals, vol. 29, pp. 127–174. Supplement: vol. 30, pp. 319–330, (1947).

———, and YOUNGQUIST, WALTER, L., 1948, American Permian nautiloids: Geol. Soc. America, Mem. 41, pp. 1–218, pls. 1–59.

NEWELL, N. D., 1936, Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma, III Cephalopoda: Jour. Paleontology, vol. 10, pp. 481–489, pls. 68–72.

STURGEON, MYRON T., 1946, Allegheny fossil invertebrates from eastern Ohio—Nautiloidea: Jour. Paleontology, vol. 20, pp. 8–37, pls. 3–9.

———, and MILLER, A. K., 1948, Some additional cephalopods from the Pennsylvanian of Ohio: Jour. Paleontology, vol. 22, pp. 75–80, pls. 18, 19.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 96–101, JANUARY 1954

NOMENCLATURAL REVIEW OF GENERA AND SUBGENERA OF CUCULLAEIDAE

DAVID NICOL
U. S. National Museum

ABSTRACT—The taxonomic validity of every generic and subgeneric name allocated to the pelecypod family Cucullaeidae is reviewed, and the type species of each acceptable genus and subgenus is given. *Arca disparilis* d'Orbigny, 1846, is a homonym of *Arca disparilis* Reeve, 1844. *Arca disparilis* d'Orbigny is here renamed *subdisparilis*, new name.

MOST living prionodonts can be divided into two large groups. Elongate shells with byssal gapes, such as those of *Arca*, *Barbatia*, and other closely allied forms, characterize the smaller group; these genera are now confined to warm water. The larger group is represented by such genera as *Anadara*, *Cucullaea*, *Noetia*, and *Glycymeris*, which do not have byssal gapes and are found in both warm and temperate waters. (Some anadarids have byssuses but not byssal gapes.) It appears that the elongate forms with byssal gapes originated at least as early as late Paleozoic time and are the more primitive; the other stock did not appear until Jurassic time. In other words, the prionodonts arose from an ancestral group attached by a byssus, and the main trend from Jurassic to Recent has been to assume a free or active mode of life (see Douvillé, 1912, pp. 463, 466).

The basic family of the second and larger group is the Cucullaeidae, and it appears that most, if not all, of the second group originated directly or indirectly from the cucullaeids. This family has had no complete revision; however, the most comprehensive discussion of it I have seen is that of Finlay and Marwick (1937, pp. 18–19). These authors give a good account of the history of the Cucullaeidae from the inception of the family in the early Jurassic until the present (one species of the entire family being extant, Nicol, 1950a).

The main problem in dealing with the cucullaeids is one of defining the limits of the family, and in a group as large and variable as the Cucullaeidae this is difficult to do. In the past most workers have erroneously defined the limits of the family mainly on the basis of the hinge teeth. Because the hinge teeth of the cucullaeids are highly variable, all morphologic characters should be considered and evaluated in order to define the family more accurately.

A résumé of the morphologic characters of the cucullaeids is as follows: prominent chevron-shaped grooves on ligament (except in the living species); prionodont teeth symmetrically arranged or nearly so; hinge teeth variable as to size and number (the two extremes are exemplified by *Pseudocucullaea* and *Trigonarca*); valves sometimes unequal, the left valve always slightly larger; valves with or without differing sculpture; radial ribs commonly present; internal ventral border with or without denticulations; posterior adductor muscle commonly on a raised buttress; valves without byssal gape.

Later work may prove that some of the genera and subgenera can be grouped into separate subfamilies or families. For example, some genera of the group of Cretaceous prionodonts with symmetrical glycymeridlike hinges, notably *Trigonarca*, *Protarca*, *Peruarca*, and *Arcullaea* have been placed in primarily Cenozoic prionodont families; but except for the hinges, these genera appear to be more nearly allied to the Cucullaeidae, and may comprise a separate subfamily or family.

Most workers have placed *Grammatodon*, *Indogrammatodon*, and *Nanonavis* in the Parallelodontidae, although the shells of these genera are quite different from the elongate parallelodontid shells and have no byssal gape. Cox (1940, pp. 40–41) also notes this discrepancy when he says:

> Although the characters of the hinge are, generally speaking, of primary importance in the classification of the Lamellibranchia, in the discussion of generic affinities some regard should also be paid to the general external characters of the shell. In the present instance the external

characters of *Grammatodon*, which is confined to the Mesozoic, differ so appreciably from those of *Parallelodon*, which ranges from the Devonian to the Jurassic, that I cannot accept the two groups as synonymous.

In the description of the subgenus *Grammatodon*, sensu stricto, Cox (1940), p. 41 makes the following statement:

> Shell of small-medium size (for the family), not greatly elongated, only slightly inequilateral, much resembling a small *Cucullaea;* carina varying from rounded to sharp.

It is obvious that the systematic position of many of the Mesozoic (primarily Jurassic) prionodont genera is incorrect because only hinge characters have been considered. My aim has been to point this out; and only a careful study of type species on which all morphological characters are considered and evaluated will solve the problems of prionodont systematics.

The following genera and subgenera are cucullaeids, with type species having morphological characters that correspond to those of the family, and names that are nomenclaturally valid. This does not mean that all will be acceptable when careful work on the classification of the Cucullaeidae is completed, but these names form a basis for future taxonomic work on the family.

Archaeodon Crickmay, 1930, p. 42. Type species (original designation) *Archaeodon phylarchus* Crickmay, 1930; Jurassic; British Columbia. Figd., Crickmay, 1930, pl. 2, figs. a–c.

Arcullaea Vokes, 1946, pp. 150–151. Type species (original designation) *Arcullaea olea* Vokes, 1946; Lower Cretaceous, Aptian; Lebanon. Figd., Vokes, 1946, pl. 1, figs. 15–22.

Ashcroftia Crickmay, 1930, p. 43. Type species (original designation) *Ashcroftia inversidentata* Crickmay, 1930; Jurassic; British Columbia. Figd., Crickmay, 1930, pl. 2, figs. d–e.

Cucullaea Lamarck, 1801, p. 116. Type species (subsequent designation, J. G. Children, 1823, p. 318) *Cucullaea auriculifera* Lamarck, 1801 = *Arca cucullata* Röding, 1798 = *Arca cucullus* Gmelin, 1791 = *Arca labiata* Solander, 1786. The type species is the sole extant representative. It lives in the Indian Ocean, the East Indies, the Philippines, Australia, and southern Japan, including the China Sea. For a discussion of the designation of the type species, see Nicol, 1950a, p. 338. Figd., Reeve, 1870, *Cucullaea* pl. 1.

Cucullastis Finlay and Marwick, 1937, p. 20. Type species (original designation) *Cucullaea* (*Cucullastis*) *barbara* Finlay and Marwick, 1937; Wangaloan, Danian; New Zealand. Figd., Finlay and Marwick, 1937, pl. 1, figs. 11, 14–16.

Cucullona Finlay and Marwick, 1937, p. 19. Type species (original designation) *Cucullaea* (*Cucullona*) *inarata* Finlay and Marwick, 1937; Wangaloan, Danian; New Zealand. Figd., Finlay and Marwick, 1937, pl. 2, figs. 2–5.

Dicranodonta Woods, 1899, p. 53. Type species (original designation) *Cucullaea donningtonensis* Keeping, 1883; Lower Cretaceous, England. Figd., Woods, 1899, pl. 10, figs. 11a–c, 12–14; pl. 11, figs. 1a–b, 2.

Grammatodon Meek and Hayden, 1860, p. 419. Type species (monotypy) *Arca* (*Cucullaea*) *inornata* Meek and Hayden, 1858; Jurassic; Black Hills, South Dakota. Figd., Meek and Hayden, 1864, pl. 3, figs. 9, 9a, 9b.

Idonearca Conrad, 1862, p. 289. Type species (subsequent designation, Dall, 1898, p. 603) *Cucullaea tippana* Conrad, 1858; Upper Cretaceous; Mississippi. Figd., Conrad, 1858, pl. 35, fig. 1. Wade (1926, p. 43), Stephenson (1941, pp. 92–94), and others consider *Cucullaea tippana* Conrad conspecific with *Cucullaea capax* Conrad, 1858.

Indogrammatodon Cox, 1937, pp. 194–195. Type species (original designation) *Cucullaea virgata* J. de C. Sowerby, 1840; Upper Jurassic; India. Figd., Cox, 1937, pl. 15, figs. 8–9.

Latiarca Conrad, 1862, p. 289. Type species (subsequent designation, Stoliczka, 1871, p. xxi) *Cucullaea gigantea* Conrad, 1830; Eocene; Prince Georges Co., Maryland. Figd., Clark and Martin, 1901, pls. 52–55.

Lopatinia Schmidt, 1872, p. 282. Type species (subsequent designation, Maury, 1930, pp. 302–303) *Pectunculus petschorae* Keyserling, 1846; Lower Cretaceous: U.S.S.R. Figd., Keyserling and Krusenstern, 1846, pl. 17, figs. 5–6.

Megacucullaea Rennie, 1936, pp. 305–308. Type (original designation) *Cucullaea kraussi* Tate, 1867; Lower Cretaceous; South Africa. Figd., Rennie, 1936, pl. 44, fig. 2.

Nanonavis Stewart, 1930, p. 68. Type species (original designation) *Arca carinata* J. Sowerby, 1813; Cretaceous, Albian; England. Figd., Woods, 1899, pl. 8, figs. 3–8.

Nordenskjöldia Wilckens, 1910, pp. 26–30. Type species (original designation) *Arca disparilis* d'Orbigny, 1846, not *Arca disparilis* Reeve, 1844. *Arca disparilis* of d'Orbigny is here renamed *subdisparilis* Nicol, new name. Upper Cretaceous; Pondicherry, India. Figd., Stoliczka, 1871, pl. 20, figs. 6, 6a, 7. D'Orbigny (1850, p. 245) considered his species *disparilis* conspecific with *Arca japetica* Forbes, 1846, a view not shared by either Stoliczka (1871, pp. 350–351) or Wilckens (1910, pp. 29–30). Unfortunately the generic name *Nordenskjöldia* Wilckens, 1910, is very similar to *Nordenskioeldia* Sahlberg, 1880, and *Nordenskiöldia* Koenike, 1907.

Peruarca Olsson, 1944, pp. 32–33. Type species (original designation) *Peruarca pectunculoides* Olsson, 1944; Upper Cretaceous, Maestrichtian; Paita region, Peru. Figd., Olsson, 1944, pl. 3, figs. 6–7.

Pettersia Nicol, 1953, pp. 103–105. Type species

(original designation) *Cardium* (?) *abnormalis* Olsson, 1944; Upper Cretaceous, Maestrichtian; Paita region, Peru. Figs., Nicol, 1953, figs. 1–5. In the original description of *Pettersia* I did not include a description of the genus under the generic heading, although that information is found at the end of the species description. *Pettersia* has an arched prionodont hinge like that of *Glycymeris*, *Peruarca*, and *Trigonarca*. The ligament has several chevron-shaped grooves like *Glycymeris*, *Trigonarca*, and *Idonearca*. The posterior adductor muscle of *Pettersia* is located on a flange which is like that of *Cucullaea* and *Idonearca*. The crenulated interior ventral margin resembles that of *Glycymeris* and many of the cucullaeids. The most distinctive feature of *Pettersia* is the presence of a well-developed sulcus which runs from the umbo to the ventral margin.

Protarca Stephenson, 1923, pp. 103–104. Type species (monotypy) *Protarca obliqua* Stephenson, 1923; Upper Cretaceous; North Carolina. Figd., Stephenson, 1923, pl. 19, figs. 1–3. This genus appears to be most closely allied to *Trigonarca* on the basis of shell morphology.

Pseudocucullaea Solger, 1903, pp. 76–77. Type species (original designation) *Pseudocucullaea lens* Solger, 1903; Upper Cretaceous; Cameroons, West Africa. Figd., Solger, 1903, p. 77; fig. 1, a, p. 78; figs. 4a, b, c, p. 79. Some workers have considered *Pseudocucullaea* a synonym of *Lopatinia*. I agree with Olsson (1934, p. 23) that the two should be distinct. The differences in size, geographic distribution, and stratigraphic distribution are considerable; and despite many morphologic similarities, *Pseudocucullaea* should be considered at least a subgenus of *Lopatinia*.

Pseudomacrodon Stoll, 1934, p. 9. Type species (monotypy) *Macrodon pictum* Milaschewitsch, 1879; Jurassic, Callovian; Pomerania, Germany. Figd., Stoll, 1934, pl. 1, fig. 12.

Trigonarca Conrad, 1862, p. 289. Type species (monotypy) *Cucullaea maconensis* Conrad, 1860; Upper Cretaceous; Alabama. Figd., Stephenson, 1923, pl. 14, fig. 10; pl. 15, figs. 1–3. Although Reinhart, 1935, pp. 50–51, places *Trigonarca* in the family Arcidae (subfamily Noetiinae), on the basis of morphologic characters it appears to be more nearly related to the Cucullaeidae. It is certainly not closely related to any of the Cenozoic arcoids.

The following names are rejected from the family Cucullaeidae. They include homonyms, synonyms, names referable to other families, names by non-binomial authors, and misspellings. This list is not considered complete, but as many original references were consulted as possible. If the original reference was not seen, this fact is indicated.

Astartopsis Wöhrmann, 1889, pp. 222–223. Not a cucullaeid; Wöhrmann, p. 235, considers the genus related to *Astarte* and *Opis*.

Astartopis Diener, 1909, p. ii. Error for *Astartopsis* Wöhrmann, 1889.

Catella Healey, 1908, p. 13. Type species not designated by Healey. Triassic; Burma. This genus is probably a parallelodontid.

Cuccullaea Tenison Woods, 1876, p. 15. Error for *Cucullaea* Lamarck, 1801.

Cuculaea Conrad, 1830, pp. 227, 230. Error for *Cucullaea* Lamarck, 1801.

Cuculea Djanélidzé, 1932, p. 2. Error for *Cucullaea* Lamarck, 1801.

Cuculina Rafinesque, 1815, p. 147. Emendation of *Cucullaea* Lamarck, 1801.

Cucullaae White, 1888, p. 21. Error for *Cucullaea* Lamarck, 1801.

Cucullaeigenus Renier, 1807, p. vii. Original reference not seen. Renier's names ending in *genus* have, in general, not been accepted by malacologists. For a good review of the subject, see Keen, 1951.

Cucullana Lichtenstein, 1818, p. 112. Type species (monotypy) *Arca* (*Cucullana*) *cucullus* Gmelin, 1791; Recent; Nicobar Islands. *Cucullana* is a subjective synonym of *Cucullaea* Lamarck, 1801.

Cucullea Rafinesque, 1815, p. 147. Error for *Cucullaea* Lamarck, 1801.

Cucullea Michelin, 1838, p. 102. Error for *Cucullaea* Lamarck, 1801. This misspelling has been made by several malacologists.

Cucullifera Conrad, 1875, p. 24. Type species (monotypy) *Haploscapha* (*Cucullifera*) *eccentrica* Conrad, 1875; Upper Cretaceous; Nebraska, North Dakota. Not a cucullaeid; probably an inoceramid.

Cuculloea Meek and Hayden, 1860, p. 419. Error for *Cucullaea* Lamarck, 1801.

Cucullopsis Chao, 1927, pp. 10–11. Type species (original designation) *Cucullopsis quadrata* Chao, 1927. Not a cucullaeid; a parallelodontid.

Curvirostrum Buckman, 1882, pp. 102–103. Type species (monotypy) *Curvirostrum striatum* Buckman, 1882; Bajocian, Jurassic; Dorsetshire, England. Not a cucullaeid; possibly a parallelodontid.

Cyphoxis Rafinesque (1818, p. 107, nomen nudum), 1819, p. 427. In 1819 Rafinesque gave a brief description of the genus and listed four species names; all of them are nomina nuda. Type species (monotypy) *Arca noae* Linné, 1758. Pictet (1855, p. 544) was, to my knowledge, the first worker who included a described species in the genus *Cyphoxis*. This was done in the following manner:

"On doit de même, réunir aux arches les *Cyphoxis*, Rafinesque (*Arca noe*), les Navicula, Blainville, etc."

There seems to be no doubt that Pictet intended that *Arca noae* Linné belonged to *Cyphoxis*. Pilsbry (1929, pp. 113–114) assigned the species *Cucullaea vulgaris* Morton, 1830, as the type species of *Cyphoxis*, but this was done without knowledge of Pictet's work. Most workers before Pilsbry's paper was published considered *Cyphoxis* a synonym of *Arca*, and

at present it appears that *Cyphoxis* Rafinesque, 1819, is an objective synonym of *Arca* Linné, 1758. Stephenson (1941, p. 90) objected to the use of *Cyphoxis* on the basis that the genotype selected by Pilsbry was a species dubium.

Cyphoxus Paetel, 1875, p. 64. Error for *Cyphoxis* Rafinesque, 1819.

Cyphoxys Agassiz, 1846, p. 113. Emendation of *Cyphoxis* Rafinesque, 1819.

Eusebia Maury, 1930, pp. 206–209. Type species (original designation) *Eusebia stantoni* Maury, 1930; Upper Cretaceous; Brazil. This genus is a subjective synonym of *Pseudocucullaea* Solger, 1903, and is a homonym of *Eusebia* Duponchel, 1845.

Gammatodan and *Gammmatodon*, Yabe, Nagao, and Shimizu, 1926, p. 44 (12). Errors for *Grammatodon* Meek and Hayden, 1860.

Glycydonta Cotton, 1936, pp. 503–504. Type species (original designation) *Venus marica* Linné, 1758. Not a cucullaeid; probably a veneroid.

Höferia Neave, 1939, p. 668. Error for *Hoferia* Bittner, 1894.

Hoferia Bittner, 1894, p. 190. Type species (original designation) *Lucina duplicata* Münster, 1838. Not a cucullaeid; probably a parallelodontid.

Macrodontella Assmann, 1916, p. 616. Type species (monotypy) *Macrodontella lamellosa* Assmann, 1916; Triassic; Germany. Possibly a parallelodontid.

Microcucullaea Iredale, 1929, pp. 159, 187. Type species (original designation) *Bathyarca perversidens* Hedley, 1902. Not a cucullaeid; probably an anadarid. See Reinhart (1935, p. 12).

Palestinarca Vokes, 1946, pp. 154–155. Type species (original designation) *Trigonarca palestina* Whitfield, 1891; Lower Cretaceous, Aptian; Lebanon. Figd., Vokes, 1946, pl. 2, figs. 1–5, text fig. 1. Not a cucullaeid. The finely striated ligament is apparently like that of the noetids.

Pichleria Bittner, 1894, pp. 189–190. Type species (original designation) *Cucullaea auingeri* Laube 1865; Upper Triassic; Austria. Not a cucullaeid; probably a parallelodontid.

Pseudogrammatodon Arkell, 1930, p. 307. Type species (original designation) *Arca adversidentata* Deshayes, 1860. Not a cucullaeid; probably an arcid.

Trigonoarca Conrad, 1867, p. 9. Error for *Trigonarca* Conrad, 1862. This misspelling was used by many later workers.

Vetoarca Stephenson, 1947, p. 165. Type species (original designation) *Vetoarca hindsana* Stephenson, 1947. Not a cucullaeid; possibly a limopsid.

ACKNOWLEDGMENTS

Mr. Druid Wilson of The Johns Hopkins University helped review the list of genera and subgenera of cucullaeids. Dr. J. B. Reeside, Jr., and Dr. R. W. Imlay of the U. S. Geological Survey showed me pertinent references. The assistance of these people is greatly appreciated.

REFERENCES

Agassiz, L., 1846, Nomenclatoris Zoologici Index Universalis, etc., 393 pp., Soloduri.

Arkell, W. J., 1930, The generic position and phylogeny of some Jurassic Arcidae: Geol. Mag., vol. 67, pp. 297–310, pls. 14–16, 14 text figs.

Assmann, P., 1916, Die Brachiopoden und Lamellibranchiaten der oberschlesischen Trias: Jahr. K. preuss. Geol. Landesanstalt, Band 36, Teil 1, Heft 3, pp. 586–638, pls. 30–36, 3 text figs.

Binney, Wm. G., and Tryon, George W., Jr., 1864, The complete writings of Constantine Smaltz Rafinesque on Recent and fossil Conchology, 96 pp., pls. 80–82, New York.

Bittner, A., 1894, Zur Kenntniss der Nuculiden und Arciden der Fauna von St. Cassian: Verh. K.-K. Geol. Reichsanstalt, Wien, Jahrgang 1894, pp. 186–191.

Buckman, S. S., 1882, On the new genus of bivalve, *Curvirostrum striatum:* Proc. Dorset Nat. Hist. Antiquarian Field Club, vol. 4, pp. 102–103, 3 text figs.

Chao, Y. T., 1927, Fauna of the Taiyuan formation of North-China—Pelecypoda: Palaeontologica Sinica, ser. B, vol. 9, fasc. 3, 64 pp., 4 pls.

Children, J. G., 1823, Lamarck's genera of shells (with plates), continued: Quart. Jour. Sci. Lit., Arts, vol. 14, no. 28, pp. 298–322.

Clark, W. B., and Martin, G. C., 1901, The Eocene deposits of Maryland: Md. Geol. Surv., Eocene vol. 331 pp., 64 pls.

Conrad, T. A., 1830, On the geology and organic remains of a part of the peninsula of Maryland: Jour. Acad. Nat. Sci. Philadelphia, vol. 6, pp. 205–230, pls. 9–10.

——, 1858, Observations on a group of Cretaceous fossil shells, found in Tippah County, Miss., etc.: Jour. Acad. Nat. Sci. Philadelphia, vol. 3, 2nd ser., pp. 323–336, pls. 34–35.

——, 1860, Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama: Jour. Acad. Nat. Sci. Philadelphia, 2nd ser., vol. 4, pp. 275–298, pls. 46–47.

——, 1862, Descriptions of new genera, subgenera, and species of Tertiary and Recent shells: Proc. Acad. Nat. Sci. Philadelphia, vol. 6, 2nd ser., pp. 284–291.

——, 1867, Descriptions of new genera and species of fossil shells: Am. Jour. Conchology, vol. 3, pp. 8–16.

——, 1875, (in Cope) The Vertebrata of the Cretaceous formations of the West: U. S. Geol. Survey Territories, vol. 2, 302 pp., 57 pls.

Cotton, B. C., 1936, A new fossil bivalve mollusc from South Australia: Records Australian Mus., vol. 5, no. 4, pp. 503–504.

Cox, L. R., 1937, Notes on Jurassic Lamellibranchia. II. On *Indogrammatodon*, a new subgenus from the Jurassic of the Indo-African Province: Proc. Malacological Soc. London, vol. 22, pt. 4, pp. 194–198.

——, 1940, The Jurassic lamellibranch fauna of Kuchh (Cutch): Mem. Geol. Surv. India,

Palaeontologia Indica, ser. 9, vol. 3, pt. 3, 157 pp., 10 pls.

CRICKMAY, C. H., 1930, The Jurassic rocks of Ashcroft, British Columbia: Univ. Calif. Pub., Dept. Geol. Sci. Bull., vol. 19, no. 2, pp. 23–74, pls. 2–7, 1 map.

DALL, W. H., 1898, Contributions to the Tertiary fauna of Florida, etc.: Trans. Wagner Free Inst. Sci. Philadelphia, vol. 3, pt. 4, pp. 571–947, pls. 23–35.

DIENER, C., 1909, The fauna of the *Traumatocrinus* limestone of Painkhanda: Mem. Geol. Surv. India, Palaeontologia Indica, ser. 15, vol. 6, mem. no. 2, 39 pp., 5 pls.

DJANÉLIDZÉ, A., 1932, Materiaux pour la géologie du Radcha 1. Les ammonites Jurassiques de Tsessi: Bull. l'inst. géol. Géorgie (Tiflis), vol. 1, fasc. 1, 34 pp., 10 pls.

DOUVILLÉ, H., 1912, Classification des Lamellibranchs: Bull. Soc. Géol. France, sér. 4, tome 12, pp. 419–467, 69 text figs., 1 table.

FINLAY, H. J., and MARWICK, J., 1937, The Wangaloan and associated molluscan faunas of Kaitangata-Green Island subdivision: New Zealand Palaeont. Bull. no. 15, 140 pp., 17 pls.

GMELIN, J. F., 1791, Caroli a Linné Systema Naturae, ed. 13, tome 1, pars 6, pp. 3021–3909, Leipzig.

HEALEY, MAUD, 1908, The fauna of the Napeng beds or the Rhaetic beds of Upper Burma: Mem. Geol. Surv. India, Palaeontologia Indica, new ser., vol. 2, mem. no. 4, 88 pp., 9 pls.

IREDALE, TOM, 1929, Mollusca from the continental shelf of eastern Australia. No. 2: Rec. Australian Mus., vol. 17, no. 4, pp. 157–189, pls. 38–41.

KEEN, A. MYRA, 1951, The molluscan names in Renier's "Tavole": Nautilus, vol. 65, pp. 8–15.

KEEPING, W., 1883, The fossils and palaeontological affinities of the Neocomian deposits of Upware and Brickhill, Cambridge. Original reference not seen.

KEYSERLING, ALEXANDER GRAF, and KRUSENSTERN, PAUL VON, 1846, Wissenschaftliche Beobachtungen auf einer Reise in das Petschora-Land, im Jahre 1843, 465 pp., 22 pls., 2 maps, St. Petersburg.

LAMARCK, J. B., 1801, Système des animaux sans vertèbres, etc., 432 pp., Paris.

LICHTENSTEIN, HINRICH, 1818, Das Zoologische Museum der Universität zu Berlin, Zweite Ausgabe, 120 pp., Berlin.

LINNÉ, KARL VON, 1758, Systema naturae, ed. 10, tomus 1, 824 pp., Holmiae.

MAURY, C. J., 1930, O Cretaçeo de Parahyba do Norte: Monographias do serviço geologico e mineralogico do Brasil, vol. 8, 305 pp., 35 pls.

MEEK, F. B., and HAYDEN, F. V., 1858, Descriptions of new organic remains collected in Nebraska Territory in the year 1857, etc.: Proc. Acad. Nat. Sci. Philadelphia, pp. 41–49.

——, 1860, Systematic catalogue with synonyma, &c., of Jurassic, Cretaceous and Tertiary fossils collected in Nebraska, etc.: Proc. Acad. Nat. Sci. Philadelphia, 2nd ser., vol. 4, pp. 417–432.

——, 1864, Paleontology of the Upper Missouri, etc.: Smithsonian Contr. Knowledge, no. 172, 136 pp., 5 pls.

MICHELIN, HARDOUIN, 1838, Sur une argile dépendant du Gault: Mém. Soc. Géol. France, tome 3, mém. 5, pp. 97–103, pl. 12.

MORTON, S. G., 1830, Synopsis of the organic remains of the Ferruginous Sand formation of the United States: Am. Jour. Sci. Arts, vol. 17, pp. 274–295; continued, vol. 18, pp. 243–250, 3 pls.

——, 1834, Synopsis of the organic remains of the Cretaceous group of the United States, 88 pp., 19 pls., Philadelphia.

NEAVE, S. A., 1939–1950, Nomenclator Zoologicus, 5 vols., Zool. Soc. London.

NICOL, D., 1945, Genera and subgenera of the pelecypod family Glycymeridae: Jour. Paleontology, vol. 19, pp. 616–621.

——, 1950, Origin of the pelecypod family Glycymeridae: Jour. Paleontology, vol. 24, pp. 89–98, pls. 20–22, 2 text figs.

——, 1950a, Recent species of the prionodont pelecypod *Cucullaea:* Jour. Washington Acad. Sci., vol. 40, pp. 338–343, 9 text figs.

——, 1953, A new prionodont pelecypod genus: Jour. Washington Acad. Sci., vol. 43, pp. 103–105, 5 text figs.

OLSSON, A. A., 1934, Contributions to the paleontology of northern Peru: The Cretaceous of the Amotape region: Bull. Am. Paleontology, vol. 20, no. 69, 104 pp., 11 pls.

——, 1944, Contributions to the paleontology of northern Peru. Part VII. The Cretaceous of the Paita region: Bull. Am. Paleontology, vol. 28, no. 111, 146 pp., 17 pls.

D'ORBIGNY, A., 1846, Voyage de l'Astrolabe et de la Zélée au Pol Sud et dans l'Oceanie, Géologie (Paléontologie) Atlas, Paris. Apparently only the atlas was ever published.

——, 1850, Prodrome de Paléontologie, etc., vol. 2, 427 pp., Paris.

PAETEL, FR., 1875, Die bisher veröffentlichten Familien- und Gattungsnamen der Mollusken, 229 pp., Berlin.

PICTET, F. J., 1855, Traité de Paléontologie, etc., 2nd ed., vol. 3, 654 pp., Paris.

PILSBRY, H. A., 1929, *Cyphoxis* Rafinesque, a Cretaceous taxodont identical with *Idonearca* Conrad: Nautilus, vol. 42, pp. 113–114.

RAFINESQUE, C. S., 1815, Analyse de la Nature, ou Tableau de l'Univers et des Corps Organises, Palerme. None of the original papers of Rafinesque was seen.

——, 1818, General account of the discoveries made in the zoology of the Western States: Am. Monthly Mag. Critical Review, vol. 4, pp. 106–107.

——, 1819, Prodrome de 70 nouveaux Generes d'Animaux découverts dans l'intérieur des Etats-Unis d'Amérique, durant l'année 1818: Jour. de Physique, de Chimie, d'Histoire Naturelle, tome 88, pp. 423–428.

REEVE, L. A., 1844, Conchologia Iconica: etc., vol. 2; 1870, vol. 17, London.

REINHART, P. W., 1935, Classification of the pelecypod family Arcidae: Bull. Musée royal d'Hist. nat. Belgique, tome 11, no. 13, 68 pp.

RENIER, S. A., 1807, Tavole per servire alla classificazione e connoscenza degli animali, Pavova. Original reference not seen.

RENNIE, J. V. L., 1936, Lower Cretaceous Lamellibranchia from northern Zululand: Ann. South African Mus., vol. 31, pt. 3, no. 9, pp. 269–391, pls. 37–55.

SCHMIDT, FRIEDRICH VON, 1872, Über die neue Gattung *Lopatinia* und einige andere Petrefakten aus den mesozoischen Schichten am untern Jenissei: Verh. Russisch-Kaiserlichen Mineralogischen Gesell. St. Petersburg, zweite serie, siebenter Band, art. 13, pp. 279–289, pl. 8.

——, 1904, "Remarks on the genus *Pseudocucullaea*": Zeitschr. Deutschen geol. Gesell. Band 56, Protokoll der Juli-Sitzung, pp. 120–121.

SOLGER, F., 1903, Über *Pseudocucullaea*, einen neuen Taxodontentypus: Zeitschr. Deutschen geol. Gesell., Band 55, Protokoll der Juli-Sitzung, pp. 76–83, 7 text figs.

STEPHENSON, L. W., 1923, Volume V. The Cretaceous formations of North Carolina. Part 1. Invertebrate fossils of the Upper Cretaceous formations: North Carolina Geol. Economic Surv., 604 pp., 102 pls.

——, 1941, The larger invertebrate fossils of the Navarro Group of Texas: Univ. Texas Pub. no. 4101, 641 pp., 95 pls.

——, 1947, New Upper Cretaceous fossils from Mississippi and Texas: U. S. Geol. Survey Prof. Paper 210-E, pp. 161–196, pls. 31–33.

STEWART, RALPH B., 1930, Gabb's California Cretaceous and Tertiary type lamellibranchs: Acad. Nat. Sci. Philadelphia, Special Pub. no. 3, 314 pp., 17 pls.

STOLICZKA, FERDINAND, 1871, Cretaceous fauna of southern India. Vol. 3, The Pelecypoda, etc.: Mem. Geol. Surv. India, Palaeontologia Indica, ser. 6, 537 pp., 50 pls.

STOLL, ELISABETH, 1934, Die Brachiopoden und Mollusken der pommerschen Doggergeschiebe: Abh. geol.-palaeont. Institut der Ernst Moritz Arndt-Universität Greifswald, Heft 13, 62 pp., 3 pls.

VOKES, H. E., 1946, Contributions to the paleontology of the Lebanon Mountains, Republic of Lebanon. Part 3. The pelecypod fauna of the "Olive Locality" (Aptian) at Abeih: Bull. Am. Mus. Nat. Hist., vol. 87, art. 3, pp. 143–215, 10 pls.

WADE, BRUCE, 1926, The fauna of the Ripley formation on Coon Creek, Tennessee: U. S Geol. Survey Prof. Paper 137, 272 pp., 72 pls.

WELLER, STUART, 1907, A report on the Cretaceous paleontology of New Jersey: Geol. Surv. New Jersey, vol. 4, Pal. ser., text and plates, 871 pp., 111 pls.

WHITE, C. A., 1888, Contributions to the paleontology of Brazil; comprising descriptions of Cretaceous invertebrate fossils, etc.: Archivos do Museu Nacional do Rio de Janeiro, vol. 7, 273 pp., 28 pls.

WHITFIELD, R. P., 1891, Observations on some Cretaceous fossils from the Beyrut District of Syria, etc.: Bull. Am. Mus. Nat. Hist., vol. 3, pp. 381–441, pls. 4–11.

WILCKENS, OTTO, 1910, Die Anneliden, Bivalven und Gastropoden der Antarktischen Kreideformation: Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903 unter Leitung von Dr. Otto Nordenskjöld, Band III, Lieferung 12, 132 pp., 4 pls.

WÖHRMANN, S. F. VON, 1889, Die Fauna der sogenanten *Cardita-* und Raibler-Schichten in den Nordtiroler und bayerischen Alpen: Jahrb. K.-K. Geol. Reichsanstalt, Wien, Band 39, 1889, pp. 181–258, pls. 6–10.

WOODS, HENRY, 1899, A monograph of the Cretaceous Lamellibranchia of England. Part I. Nuculanidae, Nuculidae, Anomiidae, and Arcidae: Palaeontographical Soc., London, vol. for 1899, 72 pp., 14 pls.

WOODS, J. E. TENISON, 1876, On some Tertiary fossils from Table Cape: Papers Proc. Rept. Royal Soc. Tasmania for 1875, pp. 13–26, 14 figs.

YABE, HISAKATSU, NAGAO, TAKUMI, and SHIMIZU, SABURÔ, 1926, Cretaceous Mollusca from the Sanchû-Graben in the Kwantô Mountainland, Japan: Sci. Reports Tôhoku Imperial Univ., ser. 2 (Geology), vol. 9, no. 2, pp. 32–76 (1)–(44), pls. 12–15 (1)–(4).

MANUSCRIPT RECEIVED MARCH 10, 1953

Published by permission of the Secretary of the Smithsonian Institution.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 102–111, 8 TEXT FIGS., JANUARY 1954

SOME FOSSORIAL MAMMALS FROM THE TERTIARY OF WESTERN NORTH AMERICA

CHARLES A. REED
College of Pharmacy, University of Illinois, Chicago 12

ABSTRACT—A clear-cut distinction is presented between the burrowing behavior of the moles (Mammalia: Insectivora: Talpidae) and the "terrier-type" digging stroke of all other hitherto-known fossorial therian mammals; these differences are reflected in morphological distinctions between the humeri of the two groups. Then follows an anatomical and functional analysis of three types of fossil humeri: an unnamed specimen from the middle Paleocene of Montana; *Cryptoryctes kayi*, genus and species new, from the early Oligocene of Montana; and *Arctoryctes terrenus* Matthew 1907, from the early Miocene of South Dakota. It is concluded that all three were talpid-like, not terrier-like, in their burrowing behavior but that none were moles, strictly speaking, or ancestral to the Talpidae. The Paleocene specimen would seem to be phylogenetically isolated, but *Cryptoryctes* may well have been ancestral to *Arctoryctes*. Convergent morphological details, as between the Paleocene form, the Oligocene-Miocene line, and the known talpids, are remarkable. The ordinal relationships of the fossil forms are unknown, although they probably belong to the Insectivora or Edentata.

INTRODUCTION

THIS paper deals with the humeri of three groups of burrowing mammals from the Paleocene, Oligocene, and Miocene, respectively, of Montana and South Dakota. None of these humeri, on close examination, could seem to belong to moles (Insectivora: Talpidae) but each has peculiar specializations which are mole-like and found in no other mammals. An introductory discussion of the burrowing mechanisms and the humeri of fossorial mammals thus becomes necessary.

All hitherto-known non-talpid therian fossorial mammals burrow by rapid anteroposterior scratching movements of the forefeet, the dirt being displaced backward and under the body; this technique has been called the "terrier" or "rapid-scratch" method (Campbell, 1938). In such animals the humerus is held and used in the position typical of small cursorial quadrupedal mammals.

The humeri of such therian "terrier-type" burrowers exhibit remarkably constant specializations (I have examined skeletons of *Vombatus*, *Manis*, *Chrysochloris*, *Orycteropus*, *Taxidea*, several genera of Dasypodidae, and many genera of burrowing rodents, and have consulted the literature for *Metacheiromys* [Simpson, 1931] and *Notoryctes* [Stirling, 1891; Carlsson, 1904]). The proximal part of the humerus is relatively unchanged, with a bulbous or slightly ovoid head lying partially between greater and lesser tuberosities, the three forming a triangle and resembling the basic pattern of cat, dog, mouse, or man. The deltoid ridge is invariably developed, and quite often the pectoral ridge also; sometimes they are joined throughout their length. The shaft tends to be round, and the teres tubercle, for the insertion of the Mm. teres major and latissimus dorsi, is not well developed. The distal end is generally broad, usually by the enlargement of the lateral epicondyle, often accompanied by a high lateral supracondyloid ridge spiralling well up onto the shaft (although in *Chrysochloris* it is the medial epicondyle that is developed). The capitulum is roller-shaped, with its long axis transverse; in shape, both capitulum and trochlea, although possibly enlarged and sturdy, are typical of almost any small therian.

The fossorial moles[1] have evolved a completely different burrowing mechanism and a humerus (fig. 1) strikingly dissimilar in morphological detail. In the living animal, the bone is held either laterally, or, in the more specialized talpids, dorsolaterally, and, while retaining the typical scapulohumeral joint, a new joint has been evolved

[1] One mole, *Uropsilus*, is primitive, shrew-like, and probably non-burrowing; its humerus, also, is shrew-like.

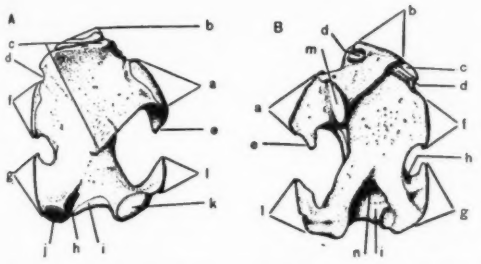


FIG. 1—*Scapanus latimanus*, left humerus, ×1.5. A. Anterior aspect. B. Posterior aspect. a, greater tuberosity; b, lesser tuberosity; c, pectoral process; d, bicipital groove; e, deltoid process; f, teres tubercle; g, medial epicondyle; h, supracondyloid (entepicondylar) foramen; i, trochlea; j, fossa for origin of great ligament of the M. flexor digitorum profundus; k, capitulum; l, lateral epicondyle; m, head; n, olecranon fossa.

between the distal end of the clavicle and the enlarged greater tuberosity. Proximally, the humerus is very wide, as wide or wider than it is distally, due to the extreme development of the greater and lesser tuberosities. The head is elongate, not round, and does not lie between the tuberosities, but has been shifted onto the posterior surface. The deltoid ridge, contrary to general opinion, is reduced. The bicipital groove, carrying the tendon of origin of M. biceps brachii, is converted into a transverse tunnel by the approximation of the lesser tuberosity and the proximal part of the pectoral process. The shaft is not round, but broad and flattened anteroposteriorly. The teres tubercle becomes greatly enlarged and elongated, as do also the lateral and medial epicondyles. A large pit on the medial epicondyle marks the point of origin of an important tendon associated with the M. flexor digitorum profundus. The capitulum and trochlea may be separate, and the former is displaced laterally; furthermore, the capitulum is an ovoid bulb with its long axis running from anterolateral to posteromedial. The olecranon pit is large and deep.

Only the burrowing moles possess a functional humero-clavicular joint and have the bicipital groove transformed into a transverse tunnel; no other humerus has these characters.

The essence of the talpid burrowing stroke consists primarily of the rotation, accompanied by retraction, of the laterally or dorsolaterally extended humerus, due to the contraction particularly of the M. teres major, inserting on the teres tubercle (Campbell, 1939; Reed, 1951). The great development of the teres tubercle provides a longer lever arm for this rotation, and the clavicular joint furnishes the necessary support, lacking in other mammals, for this powerful rotation and retraction. The recovery stroke, instigated by the pectoral musculature, is aided by the M. biceps brachii, whose contraction not only flexes the forearm but, due to its peculiar course through the previously mentioned tunnel across the proximal end of the humerus, counter-rotates the humerus into its original position (fig. 2). Another important factor in the talpid burrowing stroke is the presence of an extremely large tendon, associated with the M. flexor digitorum profundus. This tendon runs from a pit on the medial epicondyle of the humerus to the palmar surface of each digit and mechanically tightens upon rotation of the humerus, thus flexing and strengthening the manus and digits during the burrowing-stroke. The whole action has been likened to the swimming movements of a man's arms during the breast-stroke, except that the mole's forelimbs are held more dorsally and the humerus is rotated to a much greater degree.

Of the three types of humeri here specifically under consideration, the one from the Paleocene, already figured and described by Simpson (1937, pp. 139–140) is somewhat broken and difficult of analysis; further discussion will be deferred until later.

The first specimen of the Oligocene form I found while collecting vertebrate fossils for the U. S. Geological Survey in the summer of 1950, at Pipestone Springs, near Whitehall, Jefferson County, Montana. The following summer, while collecting for myself at the same locality, I found parts of two more humeri of the same unknown genus, which I here propose as new.

CRYPTORYCTES[2] Reed, gen. nov.

Type.—*Cryptoryctes kayi* Reed, n. sp.

Distribution.—Chadronian, Oligocene, Montana.

[2] Κρυπτός, hidden; Ορυκτης, a digger. The name is partially in reference to the fact that this animal has long been "hidden" from discovery, and also refers to the hidden or unknown nature of its relationships.

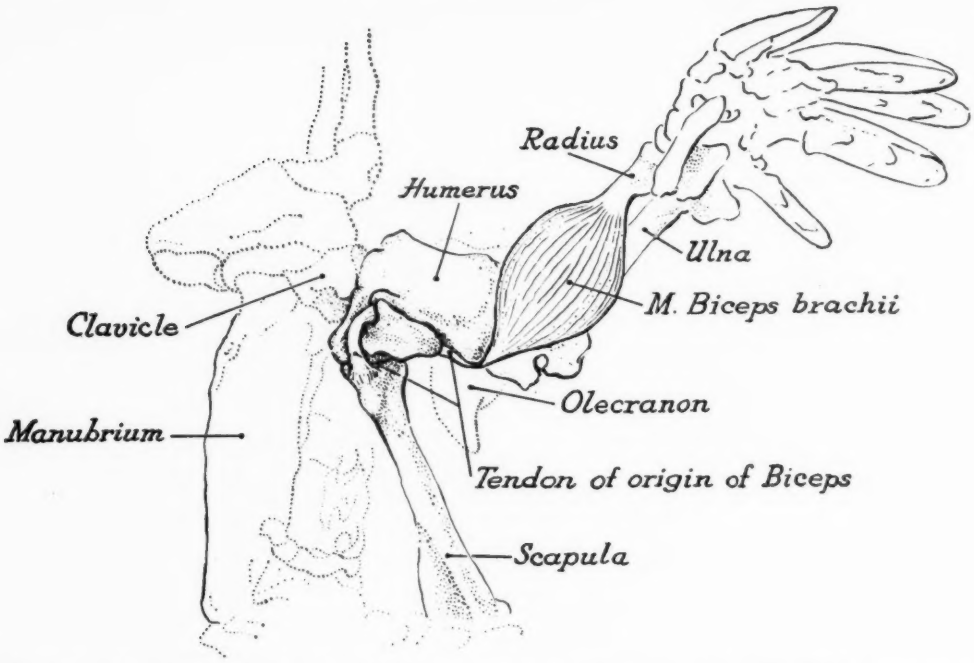


FIG. 2—Left pectoral region and associated skeleton of a mole, *Scapanus latimanus*. Contraction of the M. biceps brachii, due to the course of its tendon of origin, tends to rotate the humerus, much as a string around a top rotates the top. Lateral view.

Diagnosis.—Humerus (figs. 3–4) flattened anteroposteriorly and broadened lateromedially; head of humerus elongated in the plane of the long axis of the bone, and placed posterolaterally as compared to its more proximomedial position in small cursorial mammals; lesser tuberosity elongated; greater tuberosity small and not specialized to form a joint with the clavicle; teres tubercle produced medially; distal end of pectoral ridge elevated into a distinct process; capitulum bulbous; capitulum and trochlea lateral in position as contrasted with the more central position in small cur-

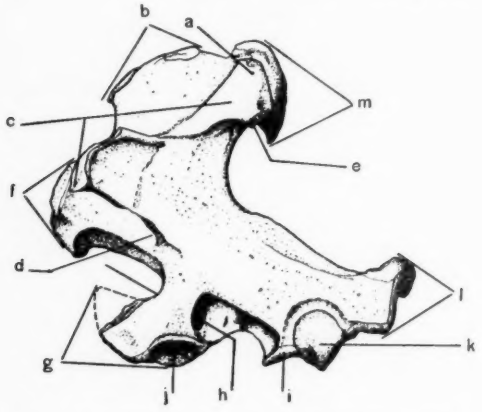


FIG. 3—*Cryptoryctes kayi*, left humerus, ×3.8. (Composite drawing). Anterior aspect. Abbreviations as in fig. *1*.

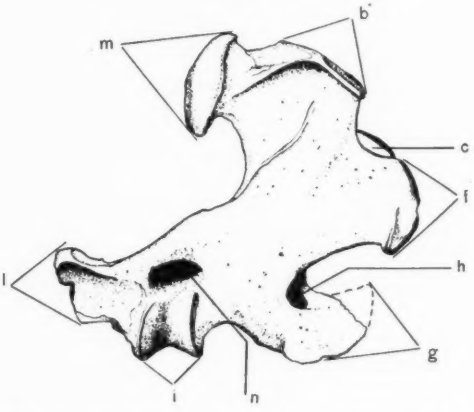


FIG. 4—*Cryptoryctes kayi*, left humerus, ×3.8. (Composite drawing). Posterior aspect. Abbreviations as in fig. *1*.

sorial mammals; lateral epicondyle produced and sculptured; medial epicondyle extended toward the teres tubercle and bearing a large pit distally; supracondyloid foramen present and elongate.

CRYPTORYCTES KAYI,[3] Reed, sp. nov.

Type.—Chicago Natural History Museum no. PM1009; a left humerus lacking lateral epicondyle, medial epicondyle, and the projection at the distal end of the pectoral ridge; collected by C. A. Reed, Aug. 24, 1951.

The hypodigm (Simpson, 1940) consists of the type, plus the following specimens: U. S. National Museum no. 19102; distal two-thirds of a left humerus; collected by C. A. Reed, Aug. 5, 1950. Chicago Natural History Museum no. PM1010; broken parts of right humerus, embedded in a coprolite; collected by C. A. Reed, Aug. 24, 1951. Carnegie Museum, Pittsburgh, Pa., numbers 8931, 8932, 8933; fragments, respectively, of one left and two right humeri; collected by LeRoy Kay.

Locality.—All specimens collected to date are from the type locality—Big Pipestone Springs, approximately 9 miles west of Whitehall, Jefferson Co., Montana; Chadronian age, early Oligocene.

Diagnosis.—Same as for the genus.

The humerus of *Cryptoryctes* cannot belong to a mole, as it possesses neither of the two characters (humero-clavicular joint or transversely tunneled bicipital groove) unique to all fossorial members of that family. However, the convergent resemblances between the humeri of *Cryptoryctes* and the fossorial talpids are marked, and would seem to indicate a similarity in function. Since the great development of the teres tubercle in the true moles is correlated with hypertrophy of the M. teres major and with humeral rotation as the major factor in the burrowing stroke, the even greater development of the teres tubercle in *Cryptoryctes* would seem to indicate similar muscle development and a similar type of burrowing stroke. Lacking, however, the humero-clavicular joint, *Cryptoryctes* must have developed some other mechanism, probably muscular and ligamentous, to support the shoulder against the powerful thrust of the laterally held and rotating humerus during the burrowing stroke. Further analysis of the mechanics of the shoulder of *Cryptoryctes* must wait discovery of the remainder of the pectoral skeleton.

The retraction and simultaneous counter-rotation of the humerus of *Cryptoryctes*, involved in the forward or recovery phase of the burrowing action, must have depended almost entirely on the pectoral musculature, in the absence of the possibility of the peculiar counter-rotating action of the M. biceps brachii found in the fossorial talpids. The Mm. spinodeltoideus, supraspinatus, and infraspinatus are also important in talpid counter-rotation, but judging from the tremendous development of the pectoral process in *Cryptoryctes*, the pectoral musculature must have been particularly hypertrophied. Possibly the Mm. cleidodeltoideus and acromiodeltoideus inserted into the pectoral process, as they do in the talpids, and also aided in extension of the humerus.

On the distal end of the humerus of *Cryptoryctes* the lateral and medial epicondyles are tremendously developed, suggesting that, as in the moles, the extensor and flexor musculatures, respectively, of the manus were hypertrophied. Likewise, as in the moles, the capitulum and trochlea are shifted laterally, and the capitulum is bulb-shaped rather than roller-shaped, which suggests that possibly the elbow-joint, as well as the twisting of the shafts of ulna and radius, were similar to the arrangement in the moles (Reed, 1951).

A last detail of similarity between the talpid humerus and that of *Cryptoryctes* is the pit on the distal end of the medial epicondyle, arguing for a similar tendinous mechanism associated with the M. flexor digitorum profundus. *Chrysochloris*, the golden "mole" of South Africa, has a similar tendon (Dobson, 1883) but no pit at the site of origin. Presumably the three forms (talpids, *Cryptoryctes*, and *Chrysochloris*) have each developed this tendon independently.

In spite of the similarities of morphology and the assumed similarities in pattern of

[3] In honor of Dr. J. LeRoy Kay, of the Carnegie Museum, whose years of collecting in the Tertiary of Montana have added immeasurably to the paleontological knowledge of the area.

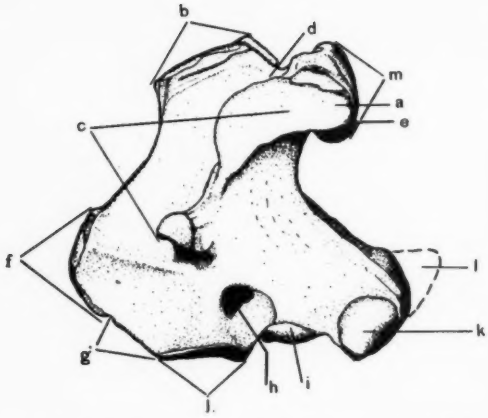


FIG. 5—*Arctoryctes terrenus*, left humerus, ×3.8. Anterior aspect. Abbreviations as in fig. *1*. Drawn from a cast of Amer. Mus. Nat. Hist. no. 12864.

function, the conclusion persists that *Cryptoryctes* was not one of the Talpidae, at least as that family has been defined on the basis of all known living and fossil material (the typical talpid humerus had already been evolved by the late Eocene; Filhol, 1877). If it be argued that a talpid could become extremely fossorial, retaining the rotatory burrowing stroke but losing the clavicular articulation and bicipital tunnel, my only answer is that in all known talpids these structures are developed in particular correlation with the degree of fossorial activity, and certainly the humerus of *Cryptoryctes* belonged to a specialized fossorial mammal (and that of *Arctoryctes*, as we shall see, to an animal even more fossorial).

The second humerus under discussion, and the only form to which *Cryptoryctes* can definitely be said to be related, is *Arctoryctes* (figs. 5–6), based on a left humerus (Amer. Mus. Nat. Hist. no. 12864) from the upper Rosebud formation, Arikareean age, early Miocene, South Dakota. This humerus was first discussed by Matthew in 1906 and *Arctoryctes* was named, without further description, in 1907. Matthew considered the humerus to belong to a chrysochlorid, and it was so listed for many years. By 1928, Matthew was not so definite concerning the chrysochlorid affinities of *Arctoryctes*, and, after a brief but non-conclusive discussion of possible relationships of the genus to the talpids and to *Apternodus*, an Oligocene solenodont, decided that it must be left as of problematical affinities. Schlaikjer (1933), who first figured the type, concluded that *Arctoryctes* was a mole. Even so, Simpson (1945) placed it *incertae sedis* in the ?Insectivora without specifying a family. Gregory (1951, vol. 2, p. 692) accepted *Arctoryctes* as a mole, and also corrected Schlaikjer's mislabeling of the pectoral process as the deltoid ridge (I differ from Gregory, however, as to the identification of the deltoid ridge in the true mole, *Scalopus*).

Probably *Arctoryctes* evolved from *Cryptoryctes;* there is nothing to indicate that it could not have. Clearly these two are more closely related to each other than either is to any other known genus. The evolutionary changes undergone by the Miocene form, as contrasted with the Oligocene, are: 1. The teres tubercle of *Arctoryctes* has shifted distally until it has fused with the medial epicondyle (a most unusual condition), and thus the action of the humeral rotators (teres major and latissimus dorsi) was applied more distally on the humerus. 2. The reduction in height and overall size of the distal, protuberant part of the pectoral process; this condition may indicate that the recovery or extensor phase of the burrowing stroke may have been taken over to a greater extent in *Arctoryctes* by the supraspinatus and/or deltoid muscles; or perhaps the origins of the pectoral musculature had

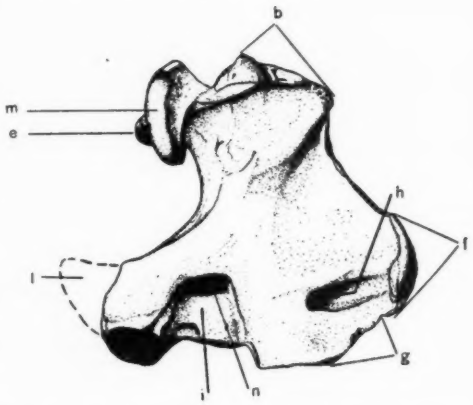


FIG. 6—*Arctoryctes terrenus*, left humerus, ×3.6. Posterior aspect. Abbreviations as in fig. *1*. Drawn from a cast of Amer. Mus. Nat. Hist. no. 12864.

migrated forward on an extended manubrium, as they have in the fossorial moles, and thus possessed a greater mechanical advantage in pulling the humerus forward and medially, with concomitant reduction in size of the process of insertion. 3. The increase in size of the pit for the origin of the tendon of the M. flexor digitorum profundus, which condition leads one to the tentative conclusion that the tendon was larger in *Arctoryctes* and the hand thus in need of greater support during a stronger burrowing stroke. Other and minor differences can readily be seen from the figures. In general the greater width of the humerus of *Arctoryctes* would argue for more efficient fossorial adaptation.

On the basis of present evidence I would say that the humeri of *Cryptoryctes* and *Arctoryctes*, in the absence of the humeroclavicular joint and the transverse bicipital tunnel, cannot belong to the Talpidae (and thus discussion of possible affinities with *Proscalops* and other known North American moles is valueless). Moreover, *Cryptoryctes* and *Arctoryctes* cannot at present be assigned to any known mammalian order, although they were probably either Insectivora or Edentata.[4] Functionally, and in a wealth of morphological detail, remarkable convergence toward the talpid humerus is indicated.

In the absence of morphologic similarity, any conjectured relationships for *Cryptoryctes* and *Arctoryctes* must be based on the more tenuous evidence of co-existence in time and of similarity in size, habitat, and geographic distribution with the forms suggested for relationship. On these admittedly poor criteria, only two groups suggest themselves for consideration: *Apternodus*, a solenodont insectivore (the possible relationship to *Arctoryctes* was first suggested by Matthew, 1928); and the Epoicotheriidae, a family of palaeanodont edentates (the possible relationship to *Arctoryctes* was first suggested by Simpson, 1927).

Of these two groups, *Apternodus* has the advantage of having been found at Pipestone Springs, since the type-species, *A. mediaevus* Matthew 1903, was described from that locality, whereas no epoicotheriid has been reported there. Other species of *Apternodus*, all based on skulls or parts of skulls, have subsequently been described from Wyoming and South Dakota; the genus ranges throughout the Oligocene. The fossorial nature of *Apternodus* was first suggested by Matthew (1928), a conclusion with which Schlaikjer has agreed (1934).

Considering size, an idea of relative proportions of small mammals can be gained from a comparison of the ratio of length of skull to length of humerus. Using the skull of *Apternodus* (*A. gregoryi* and *A. brevirostris*; Schlaikjer, 1933, 1934) and the humeri of *Cryptoryctes* and *Arctoryctes*, this skull/humerus ratio is 424% and 409%, respectively. These ratios would seem disproportionate, even for a fossorial or semifossorial animal, since the same ratios in a series of other small mammals are as follows (skull and humerus from same individual in each case): *Metacheiromys* (data from Simpson, 1931), 137%; *Scapanus*, 229%; *Condylura*, 245%; *Sorex*, 248%; and *Neurotrichus*, 304% (this skull is known to be relatively long for its body size; Reed, 1951). However, *Apternodus altitalonidus* Clark (1937), based only on a fragmentary lower jaw, is considerably smaller than other known apternodontines and probably also smaller than *Cryptoryctes* or *Arctoryctes*, so that the possible association of these three genera should not be discounted on the basis of disparity in size. True, *Apternodus* has never been recorded from the Miocene, but the discovery of a species in the late Oligocene (Macdonald, 1951) narrows the time-gap considerably.

The epoicotheriid edentates are at present known only from two skulls, each the type of a monospecific genus; *Epoicotherium* Simpson 1927 (*Xenotherium unicum* Douglas 1905) is from the Chadronian of McCarty's Mountain, Madison Co., Montana, and *Xenocranium pileorivale* Colbert 1942 is probably from the Orellan[5] of Hat Creek

[4] Actually, in the absence of intermediate forms, it is impossible, on the basis of the humerus alone, to determine the ancestry of a specialized fossorial mammal; for instance, the derivation of such "advanced" moles as *Talpa*, *Scapanus*, or *Scalopus* from shrew-like ancestors could not be determined from a comparison of humeri alone, lacking the intermediate stages (Campbell, 1939; Reed, 1951).

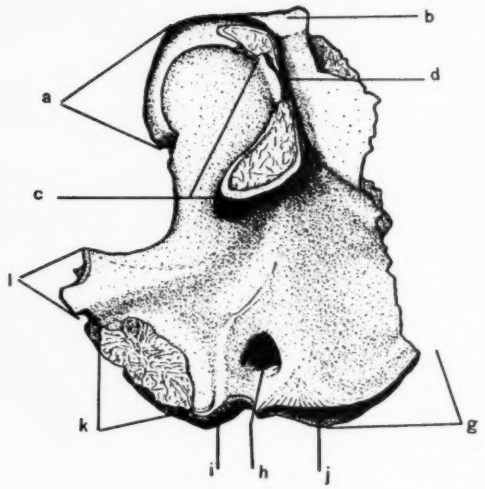


FIG. 7—U. S. National Museum no. 9777, right humerus, ×3.8. Anterior aspect. a, greater tuberosity (?); b, lesser tuberosity; c, pectoral (or deltoid?) process; d, bicipital groove; g, medial epicondyle; h, supracondyloid (entepicondylar) foramen; i, trochlea; j, elongated pit, possibly the site of origin of the great ligament of the M. flexor digitorum profundus; k, base of the broken capitulum; l, lateral epicondyle.

Basin, eastern Wyoming. The skull of *Xenocranium* is somewhat incomplete and its length must be estimated, thus invalidating further the somewhat questionable use of skull/humerus ratios, but, even so, the comparisons are given: *Epoicotherium* skull/*Cryptoryctes* humerus, 306%; *Xenocranium* skull/*Arctoryctes* humerus, 319%.

One can only say of these figures that, from what is known of the various skulls and humeri under discussion, *Cryptoryctes* and *Arctoryctes* represent animals of a size that might have fitted into either the Apternodontinae or Epoicotheriidae. Arguing against epoicotheriid affinities is the narrow time-span (early and ?middle Oligocene) of this family, at least as it is known, and the fact that no epoicotheriid fragment has been identified at Pipestone Springs, whereas humeri of *Cryptoryctes* are not too rare there, if one is really looking for them.

The third type of fossil humerus (figs. 7–8) to be discussed here is that of an unnamed specimen (United States National Museum no. 9777) of Torrejonian age (Ft. Union Series), middle Paleocene, Sweetgrass County, Montana. This is a right humerus, with the medial side broken away, and also lacking the capitulum, the tip of the lateral epicondyle, the crest of the pectoral process, and (if my interpretation is correct) the head. Any analysis of such a fragment as is left must be made and accepted with due caution.

This humerus is most unusual in many ways, but fundamentally is of the same broad type as we find in talpids and in *Cryptoryctes* and *Arctoryctes*, and thus differs from humeri of the "terrier-type" burrowers. From the size and extent of the broken medial surface I am forced to the conclusion that a large teres tubercle was present and also that, as in *Arctoryctes*, it was fused with the medial epicondyle. As stated, this condition is most unusual in mammals

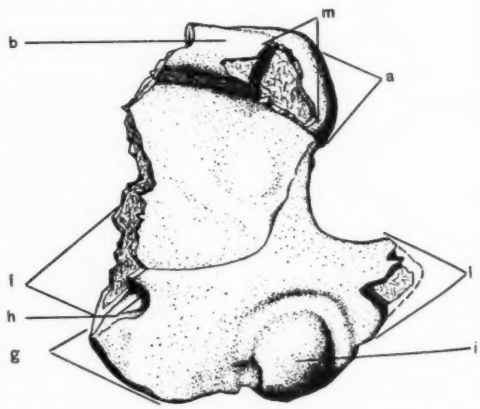


FIG. 8—U. S. National Museum no. 9777, right humerus, ×3.5. Posterior aspect. f, assumed site of broken teres tubercle; m, site where head is assumed to have broken away; other abbreviations as in fig. 6.

[5] Unfortunately the exact age of the type specimen of *Xenocranium pileorivale* must remain in doubt. According to a personal communication from Robert G. Chaffee, leader of the expedition on which the skull was collected, "In answer to your inquiry concerning the stratigraphic position of *Xenocranium*, I should like to say that the specimen probably came from the *Oreodon* beds (Orellan age). The exact position could not be determined since the specimen was brought into camp by an inexperienced member of the party who could not remember where he had picked up that particular piece. However, we had been working the *Oreodon* beds almost exclusively and the probabilities are that the specimen is of Orellan age."

TABLE *1*—COMPARATIVE MEASUREMENTS (IN MM.)

	Total length	Proximal breadth	Distal breadth	Shaft breadth (proximal to teres tubercle)	Shaft breadth (distal to teres tubercle)
U.S. Nat. Mus. no. 9777	13.9				
Cryptoryctes (Holotype)	10.9	6.0	(estimate) 10.9	3.6	3.6
Cryptoryctes Carn. Mus. no. 8931					3.8
Cryptoryctes Carn. Mus. no. 8932				3.3	3.4
Cryptoryctes Carn. Mus. no. 8933		5.6			
Cryptoryctes U. S. Nat. Mus. no. 19102					3.4
Arctoryctes (Holotype)	11.3	6.8	(estimate) 13.2	4.8	

(never having been achieved in talpids) and would argue for extreme fossorial specialization. The position of the posterior opening of the supracondyloid foramen, quite as in *Arctoryctes*, would also argue for fusion of the teres tubercle and the medial epicondyle (although in the echidna, *Tachyglossus*, the supracondyloid foramen has this same general aspect; it is due in the echidna to the great expansion of the medial epicondyle, the teres tubercle not being involved). I conclude, therefore, that this Paleocene humerus was used in a fashion comparable to that of the moles—held laterally or dorsolaterally and rotated on its own long axis, probably primarily by the action of a hypertrophied M. teres major, aided by the Mm. latissimus dorsi and subscapularis.

In other mammals with this type of rotatory action the head of the humerus has invariably been elongated and shifted onto the posterior surface. In this particular specimen, precisely where it would be usual to find such a type of head, there is instead a large broken area, suggesting that the projecting head has been broken off (compare fig. 8 with figs. 1B, 4, and 6).

If this conjecture as to the position of the head is correct, the proximo-lateral surface which Simpson regarded as the head is in reality the greater tuberosity, and if so presents a puzzle, for examination shows that it was a functional articular surface and resembles nothing so much as the talpid greater tuberosity, which articulates with the clavicle.

Is this, then, an independent development of the talpid-type humero-clavicular joint? The evidence is suggestive only, not conclusive. If Simpson is right in his designation of the head, the arm would have to be held in an extremely awkward position, in which the burrowing stroke would necessarily be forward and inward, not backward and outward. Furthermore, if he is right, the head has joined so thoroughly with the greater tuberosity that no trace of a distinction remains.

What I am calling the pectoral process may be regarded by others as the deltoid ridge; there is only the one ridge, the proximal part of which is very narrow (suggesting that it does not represent a fusion of pectoral and deltoid ridges), and its position adjacent to the bicipital groove would indicate that it is the pectoral process. Unfortunately, the large distal projecting part is broken off, quite as in most of the known humeri of *Cryptoryctes*. This distal projecting part of the pectoral ridge swings laterally instead of medially as in *Cryptoryctes* and *Arctoryctes*, but the distal part of the homologous ridge in the advanced talpids also extends laterally. The great develop-

ment of the pectoral process in this unnamed specimen, similar to that in *Cryptoryctes* and *Arctoryctes*, would argue a similar function, that of insertion for the pectoral musculature responsible for extending and adducting the humerus after the burrowing stroke.

The shaft is broad and flat, as in the talpids and the *Cryptoryctes-Arctoryctes* line, and as in these there is a distal pit medially which may have served for the site of origin of a large tendon associated with the M. flexor digitorum profundus, although here the pit is shallower and more elongate than in any other form observed. The capitulum has been broken off, but it was placed laterally and the extent and shape of the scar would indicate that it was an ovoid bulb with its long axis tilted quite as in a mole. The trochlea, however, is quite unusual. It is typical but only faintly marked anteriorly; posteriorly, instead of the expected trough ending in an olecranon fossa, there is a rounded bulb surrounded by a shallow groove, and no olecranon fossa whatever. I know of no other therian mammal that possesses such a trochlea; the distal articular surface in the echidna is ridged posteriorly and has no olecranon fossa, but the whole aspect of the humerus is otherwise entirely different and there is little suggestion of basic similarity. The South American anteater, *Myrmecophaga*, has no olecranon fossa, which means that its ulna cannot be completely extended, but such an arrangement would be most peculiar in an animal which would seem to be as specialized a burrower as was this Paleocene form.

Lacking a transverse bicipital tunnel, and with such a strange trochlea, I cannot believe that this Paleocene humerus belonged to a talpid, in spite of the possibility that a humero-clavicular joint had been evolved. Nor does it seem to present other than parallel resemblances to *Cryptoryctes* and *Arctoryctes*.

It is Simpson's opinion, undoubtedly correct, that this Paleocene humerus was in life a part of the same animal as some one of the named jaws removed from the same quarry. Unfortunately, the fragmentary nature of these jaws and skull-remnants does not allow conclusions as to the locomotor behavior of the once-living animals. None of the families involved are known to have lived into the Oligocene, except for the Leptictidae, and no leptictid is known to have shown fossorial tendencies (see Simpson, 1937, for details of the possible relationships). Any probability of familial continuity with *Cryptoryctes* and *Arctoryctes*, or with the talpids, would thus seem to be lacking.

ACKNOWLEDGMENTS

I am greatly indebted to the Department of Geology of the U. S. National Museum, for the loan of their specimens 9777 and 19102; to Dr. LeRoy Kay of the Carnegie Museum for working through a mass of unsorted material and finding three humeri of *Cryptoryctes kayi* for this study; and to the Chicago Natural History Museum, for free use of their osteological collection. I am particularly indebted to the staff of the Department of Geology and Paleontology of the American Museum of Natural History, for the considerable effort involved in making a perfect cast of the humerus of *Arctoryctes* for my use in this study.

SUMMARY

A clear-cut distinction is presented between the burrowing behavior of the moles (Insectivora: Talpidae) and the "terrier-type" digging stroke of all other hitherto-known fossorial therian mammals; these differences are reflected in morphological distinctions between the humeri of the two groups. Then follows an anatomical and functional analysis of three types of fossil humeri: an unnamed specimen from the middle Paleocene of Montana; *Cryptoryctes kayi*, genus and species new, from the early Oligocene of Montana; and *Arctoryctes terrenus* Matthew, 1907, from the early Miocene of South Dakota. It is concluded that all three were talpid-like, not terrier-like, in their burrowing behavior but that none were moles, strictly speaking, or ancestral to the Talpidae. The Paleocene specimen would seem to be phylogenetically isolated but *Cryptoryctes* could have been ancestral to *Arctoryctes*. Convergent morphological details, as between the Paleocene form, the Oligocene-Miocene line, and the known talpids, are remarkable. The ordinal relationships of the fossil forms are unknown, although they probably belong to the Insectivora or Edentata.

ADDENDA

Since the present paper was written, two

publications have appeared, bearing upon the material here presented. Galbreath (1953) mentioned three humeri, assigned provisionally to *Arctoryctes*, from the middle Oligocene of Colorado. Subsequent examination of these specimens by myself indicates that they are morphologically intermediate between *Cryptoryctes* and *Arctoryctes*, but more similar to the latter. These humeri will be discussed more fully in a later paper. Another small fossorial humerus, possibly of *Cryptoryctes*, was found by Galbreath (personal communication) in the early Oligocene of Colorado, but was blown away before it could be wrapped, and was never recovered.

Gazin (1952) has described from the early Eocene of Wyoming a new edentate genus, *Pentapassalus*, provisionally assigned to the Epoicotheriidae. The humerus of *Pentapassalus*, although in several ways quite unique, is that of a highly fossorial animal, but one that burrowed by the "terrier" method. If *Pentapassalus* is an epoicotheriid, its humerus would indicate that this family by the early Eocene had already become extremely fossorial in a way that would probably preclude close relationship with *Cryptoryctes* or *Arctoryctes*.

The late Eocene age claimed by Filhol (1877) for the earliest known talpids, and quoted by me in this paper, is open to question. Lavocat (1951) assigns these fossil moles (now known as *Geotrypus antiquus*) from the Phosphorites of France to the early Oligocene.

GALBREATH, EDWIN C. 1953, A contribution to the Tertiary geology and paleontology of northeastern Colorado: Univ. Kansas Paleont. Contr., Vertebrata, vol. 4, pp. 1–120, 26 figs., 2 pls.

GAZIN, C. LEWIS, 1952, The lower Eocene Knight formation of western Wyoming and its mammalian faunas: Smithsonian Misc. Coll., vol. 117, no. 18, pp. i-vi, 1–82, 6 figs., 11 pls.

LAVOCAT, R., 1951, Révision de la faune des mammifères Oligocènes d'Auvergne et du Velay: pp. 1–155, 27 pls. Editions "Sciences et Avenir," Paris.

LITERATURE CITED

CAMPBELL, BERRY, 1938, A reconsideration of the shoulder musculature of the Cape golden mole: Jour. Mamm., vol. 19, pp. 234–240, 1 fig.

——, 1939, The shoulder anatomy of the moles: A study in phylogeny and adaptation: Amer. Jour. Anat., vol. 64, pp. 1–39, 62 figs.

CARLSSON, ALBERTINA, 1904, Zur Anatomie des *Notoryctes typhlops:* Zool. Jahrb., Abt. f. Anat. u. Ontog., vol. 20, pp. 81–122, 4 figs., pls. 6–7.

CLARK, JOHN, 1937, The stratigraphy and paleontology of the Chadron formation in the Big Badlands of South Dakota: Ann. Carnegie Mus., vol. 25, pp. 261–350, 12 figs., pls. 21–26.

COLBERT, EDWIN H., 1942, An edentate from the Oligocene of Wyoming: Not. Nat., no. 109, 16 pp., 3 figs., 1 pl.

DOBSON, G. E., 1883, A monograph of the Insectivora, systematic and anatomical: Pt. II: pp. 86a–172, pls. 8–22. (John van Voorst, London).

FILHOL, H., 1877, Considérations sur la découverte de quelques mammifères fossiles appartenant à l'epoque Eocène supérieure: Bull. Soc. Philomath., ser. 7, t. 1, pp. 51–54.

GREGORY, WILLIAM K., 1951, Evolution emerging: A survey of changing patterns from primeval life to man: Vol. 2, pp. i–vii, 1–1013. (The Macmillan Company, New York.)

MACDONALD, J. R., 1951, Additions to the Whitneyan fauna of South Dakota: Jour. Paleontology, vol. 25, pp. 257–265, 4 figs.

MATTHEW, W. D., 1903, The fauna of the *Titanotherium* beds at Pipestone Springs, Montana: Bull. Amer. Mus. Nat. Hist., vol. 19, pp. 197–226, 19 figs.

——, 1906, Fossil Chrysochloridae in North America: Science, n.s., vol. 24, no. 624, pp. 786–788.

——, 1907, A lower Miocene fauna from South Dakota: Bull. Amer. Mus. Nat. Hist., vol. 23, pp. 169–219, 26 figs.

——, 1928, *Xenotherium* an edentate: Jour. Mamm., vol. 9, pp. 70–71.

REED, CHARLES A., 1951, Locomotion and appendicular anatomy in three soricoid insectivores: Amer. Midl. Natur., vol. 45, pp. 513–671, 34 figs.

SCHLAIKJER, ERICH M., 1933, Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. I. A detailed study of the structure and relationships of a new zalambdodont insectivore from the middle Oligocene: Bull. Mus. Comp. Zool., Harvard Coll., vol. 76, pp. 1–27, 7 figs., 1 pl.

——, 1934, A new fossil zalambdodont insectivore: Amer. Mus. Novit., no. 698, 7 pp., 3 figs.

SIMPSON, GEORGE G., 1927, A North American Oligocene edentate: Ann. Carnegie Mus., vol. 17, pp. 283–298, pl. 24.

——, 1931, *Metacheiromys* and the Edentata: Bull. Amer. Mus. Nat. Hist., vol. 59, pp. 295–381, 23 figs.

——, 1937, The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas: Bull. U. S. Nat. Mus., no. 169, pp. i–x, 1–287, 80 figs., 10 pls.

——, 1940, Types in modern taxonomy: Amer. Jour. Sci., vol. 238, pp. 413–431.

——, 1945, The principles of classification and a classification of mammals: Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i–xvi, 1–350.

STIRLING, E. C., 1891, Description of a new genus and species of Marsupialia, "*Notorycytes typhlops*": Tran. Roy. Soc. South Australia, vol. 14, pp. 154–187, pls. 2–9.

MANUSCRIPT RECEIVED NOV. 27, 1952

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, PP. 112–119, 6 TEXT FIGS., JANUARY 1954

PALEONTOLOGICAL NOTES

A NEW TECHNIQUE FOR MAKING SECTIONS OF INVERTEBRATE FOSSILS

CARL O. DUNBAR
Yale University, New Haven, Conn.

This note is written to call attention to a paper just received, by Professor Rokurô Morikawa of the Department of Earth Sciences, Saitama University, Urawa, Japan. It describes an amazing new technique for making thin sections of fossils, but since it is in the Japanese journal, *Geology*, (vol. 59, no. 689, 1952, pp. 59–62) it is likely to escape attention of American paleontologists. Although written in Japanese, it is well illustrated and an 8-line English abstract will make the method easily understood. The abstract is as follows:

A METHOD OF OBSERVATION FOR FUSULINIDS BY "SUMP-FIGURES"

This method is to be attempted [to show] that fusulinid specimens are observable by means of impressions upon celluloid membrane ("Sump-figures") without making thin slices.

The process is as follows:

1. Polish materials with a grinding machine to flatten the surfaces.
2. Immerse them in 2% HCl for 2–3 minutes.
3. Polish the material with chromium oxide or red ochre on a woolen buffer.
4. Etch them with 2% acetic acid for 1–2 minutes.
5. Make impressions upon celluloid membrane with amil acetate.

This is, of course, a modification of the collodian peel technique, but it has obvious advantages over the latter. Specimens accompanying this paper show excellent detail and prove that the method is applicable to corals and other invertebrate fossils just as well as to fusulinids.

NOTE ON SOME FOSSILS FROM THE GIRÓN GROUP IN THE RIO LEBRIJA VALLEY, DEPARTMENT OF SANTANDER, COLOMBIA

WERNER D. BRÜCKNER
University College of the Gold Coast

ABSTRACT—Fern leaves of the *Callipteridium* group and ostracods of the genus *Darwinula*, indicating a Permo-Carboniferous age, were found in the lower half of the Girón group in Santander, Colombia. This is an almost barren series of clastic, continental sediments, which are considered to be of Mesozoic age. This finding calls for renewed investigations.

The Girón group of Colombia consists of a thick series of hard, red, green, grey, or white coloured coarse to fine-grained clastic sediments of continental character. Rocks of this group are widely exposed in the Eastern Cordillera, in the Sierra Nevada de Santa Marta, and to a lesser extent in the Central Cordillera. Fossils are extremely rare in this group, and therefore the few that the author has found on the western side of the Eastern Cordillera are of some importance. The discovery was made at a point in the Rio Lebrija valley about 15 km. northwest of Bucaramanga, the capital town of the Department of Santander. A short distance upstream from the station Las Palmas of the Puerto Wilches-Bucaramanga railroad (Ferrocarril Central de Norte, sección primera), between km. posts 99 and 100 on the track, the Quebrada de Palmas enters the Rio Lebrija. The valley of this tributary cuts through the upper portion of the lower half of the Girón group. At a distance of about 1000 meters from the mouth of this stream, the Girón series includes a few layers about 10 to 20 cm thick of black, carbonaceous, slightly micaceous shale, which stand out very clearly from the common red and grey

to green coloured beds of the group. In some blocks derived from these black layers fairly well-preserved fern leaves were found. Another block contained numerous yellow grains which have been recognized as the internal moulds of ostracods.

The fossil remains have been shown to specialists in these two groups at the Senckenbergische Naturforschende Gesellschaft in Frankfort-on-the-Main (Germany). Prof. R. Kraeusel has determined the fern remains and Dr. E. Triebel the ostracods.

Prof. Kraeusel is convinced that the fern remains belong to a species of the *Callipteridium* group. The specimens were also shown to Prof. W. J. Jongmans (Heerlen, Holland), who is of the same opinion. This fern group is known from the Carboniferous, and Prof. Kraeusel maintains that it is certainly not younger than Permian.

Dr. Triebel has found that the most frequent form among the ostracod specimens belongs to the genus *Darwinula*—inhabitants of fresh to brackish water, and known from the Carboniferous onwards. Besides this smooth and elongated genus, a few sculptured ostracod moulds are present, but they could not be determined. Up to date, the association of *Darwinula* with sculptured species similar to the forms in question has only been found in the Carboniferous, but it must be admitted that the information available on the ostracod associations of Permian and Triassic formations is not sufficient to allow for a sure age determination.

Therefore, it seems that the fossiliferous beds of Palmas are of Carboniferous, or possibly of Permian age. This is, however, not in agreement with an Upper Triassic or younger age which is generally assigned to the Girón group since some ganoid fish scales have been discovered in the La Quinta formation, the Venezuelan equivalent of the Girón group (see E. Kuendig: The precretaceous rocks of the Central Venezuelan Andes . . . , Boletin de Geol. y Min., pt. 2, p. 21, Caracas, 1938). It is therefore necessary to find an explanation for this discrepancy. There is the possibility that the Palmas fossils do not really come from the black shale intercalations in the Girón group outcropping on the stream banks, but from an exposure of the underlying Carboniferous which has been overlooked. This is, however, improbable, as the nearest known Carboniferous outcrops occur at Bocas, about 9 km. upstream in the Rio Lebrija valley; and these beds are separated from those exposed in the Quebrada de Palmas by nearly 2000 meters of conformable Girón beds. The only other explanation is that in Santander the lower portion of the Girón group belongs to the Permo-Carboniferous, whereas the upper portion of the group may be Triassic or even younger. It is obvious that further investigation is necessary to decide which is the correct explanation.

The paleontological material is recorded in this paper by kind permission of the Socony-Vacuum Oil Company, Inc. The views put forward by the author are entirely his own. He wishes, however, to express his gratitude to all his helpers in Colombia, and especially to Prof. R. Kraeusel and Dr. E. Triebel for their study of the fossils.

THE STRATIGRAPHIC SIGNIFICANCE OF A CRINOID FROM THE REDWALL LIMESTONE OF ARIZONA

ARTHUR L. BOWSHER
U. S. National Museum, Washington, D. C.

Well preserved heads of *Physetocrinus* have been reported from the Redwall limestone of Arizona (Stoyanow, 1936, p. 512). The writer had an opportunity to examine Stoyanow's echinoderms from the Redwall limestone several years ago. They included a single specimen of *Physetocrinus* from Natural Bridge, Arizona. Dr. Stoyanow very graciously presented this interesting specimen to the U. S. National Museum. This note is concerned with the significance of that specimen.

The *Physetocrinus* is preserved as a mold in fossiliferous, light reddish brown chert.

Mr. L. F. Brady collected the crinoid about 27 years ago from Natural Bridge, Arizona, but the exact location was never recorded. According to W. H. Easton (oral communication) the most probable source of this specimen is a prominent dip-slope exposure at Natural Bridge, Arizona. He stated that the cherts in the Redwall at the locality are similar to the piece of chert containing the mold. Most of the fossils from there, which are not numerous, are from the top part of the Redwall limestone. Stoyanow (1936, p. 512), referring to the Natural Bridge area, wrote that the Redwall beds are composed of light gray, crinoidal, partly crystalline, and in places silicified and cherty limestone. He informed the writer that he has seen similar specimens in situ and in the same stratum at different points between Pine and the East Verde crossing (letter, May 1949).

The crinoid from Natural Bridge is conspecific with *Physetocrinus lobatus* Wachsmuth and Springer (1897, p. 599, pl. 63, figs. 8a–b). A photograph of a black rubber cast from the chert mold is reproduced herein as figure 2. The mold is shown in figure 3. A photograph of one of the two cotypes of *P. lobatus* is presented as figure 1. This is the specimen illustrated by Wachsmuth and Springer (1897) as figure 8a on plate 63. The diagnostic characters of this species are the flat tegmen with the anal opening on the surface of the tegmen, plates of the interradial areas connected with the tegmen, arms grouped at the top of each ray, rays widely separated at arm level giving the tegmen a pentagonal outline, strong compound ridges on the basal and radial plates, and strong radiating ridges on other plates of the cup.

The types of *P. lobatus* are from Lake Valley, New Mexico (Wachsmuth and Springer, 1897, p. 599). The Mississippian strata at Lake Valley belong to the Caballero and Lake Valley formations (Laudon and Bowsher, 1949, pp. 58–61). The Caballero formation is believed to be Kinderhookian in age and equivalent to the Chouteau limestone of Missouri. The Lake Valley formation consists in ascending order of the Andrecito, Alamogordo, Nunn, Tierra Blanca, Arcente, Dona Ana, and Kelly members. The Andrecito, Alamogordo, and Nunn members are believed to be lower Osagian in age and equivalent to the Fern Glen formation of Missouri. The overlying portion of the Lake Valley formation is believed to be lower Osagian and equivalent to the lower Burlington limestone of Missouri. The majority of the fossils from the Lake Valley locality have come from the Nunn member (Laudon and Bowsher, 1949, p. 13). Wachsmuth and Springer (1897, p. 599) called these crinoid-producing beds at Lake Valley the lower Burlington limestone. Some speci-

EXPLANATION OF FIGURES

FIGS. *1–3—Physetocrinus lobatus* Wachsmuth and Springer. *1*, Photograph of one of the two cotypes of *P. lobatus*, USNM no. S1258, from Lake Valley, New Mexico (Nunn member, Lake Valley formation, Osage series, Lower Mississippian). Right anterior view. Same view as shown by Wachsmuth and Springer, 1897, pl. 63, fig. 8a. ×1. *2*, Photograph of a latex cast from the mold shown in figure *3*. Left anterior view of *P. lobatus*. ×1. *3*, Photograph of chert mold of anterior, left anterior and part of posterior of *P. lobatus* from the Redwall limestone, Natural Bridge, Arizona. USNM no. 118034. ×1.

mens from the Nunn member are conspecific with lower Burlington forms. However, many of the fossils from the Alamogordo and Nunn members can be matched species for species with forms from the lower shaly part of the Fern Glen formation from Fern Glen Station, Missouri. It was to the fauna of the Nunn member that Weller referred (1909, p. 326) in correlating the Fern Glen with the Lake Valley beds. The writer agrees with Weller that the Fern Glen fauna, and its counterpart from the Nunn member of the Lake Valley formation, foreshadow the beginning of the succeeding life of the lower Burlington. The writer does not agree with Wachsmuth and Springer (1897, p. 599) that the Lake Valley beds (Nunn member) are lower Burlington in age. They are believed to be slightly older than lower Burlington but definitely Osagian in age.

Physetocrinus lobatus is diagnostic of the Nunn member of the Lake Valley formation in southern New Mexico. It is most common in the lower part of the member but is rare in the underlying Alamogordo and the overlying Tierra Blanca members of the Lake Valley formation. This crinoid is readily recognized and very different from any known in older or younger beds than the Nunn member and its correlatives. For this reason the top beds of the Redwall limestone at Natural Bridge, which have yielded *P. lobatus*, are believed to correlate with the Nunn member of the Lake Valley formation of New Mexico. They are also indirectly correlated with the Fern Glen formation of Missouri. On the basis of this crinoid, the writer believes these top beds of the Redwall limestone at Natural Bridge, Arizona to be lowermost Osagian in age but slightly older than the lower Burlington of Missouri.

Easton and Gutschick (1953) have analyzed the fauna from the top beds of the Redwall limestone near Natural Bridge and conclude that some of the fossils appear to be Kinderhookian and others Osagian in age. This discordance may be more fictitious than real. It is probable that different elements of the fauna indicate different ages. The age of any fossil or any faunule is obtained by comparison with a fossil or faunule from strata of known age. The one important reference sequence for Lower Mississippian fossils is the Chouteau limestone of Missouri. The writer believes that this discordance results from loose application of the names Chouteau limestone, Chouteau formation and Chouteau group in Missouri. Many fossils are described from the "Chouteau" of this area. The "Chouteau" is considered to be Kinderhookian, hence the "Chouteau" fossils have been accepted unequivocally by many workers as Kinderhookian in age. However, this generalization will not hold. Branson (1938) included nearly all pre-Burlington Mississippian strata, Compton limestone, Sedalia dolomite, Fern Glen formation, and Pierson limestone etc., in the Chouteau formation. Clark and Beveridge (1952) included in ascending order the Compton limestone, the Northview-Sedalia shale and dolomite, and the Pierson limestone in the Chouteau group. Some workers have considered the Pierson limestone to be Kinderhookian while others believe it to be Osagian in age. Spreng (1952) concluded that it is Osagian in age and probably correlative to the Alamogordo member of the Lake Valley formation of New Mexico. Clark and Beveridge (1952) believe it to be in part equivalent to the Fern Glen and St. Joe formations, which are Osagian in age. The fauna of the "Chouteau" is a composite one, including almost certainly fossils from both Kinderhookian and Osagian strata, but is nevertheless considered a Kinderhookian fauna. It is not surprising then that elements of the fauna from the Redwall limestone, which are compared to those of the composite "Chouteau" fauna, are in discord concerning age. Perhaps when the distribution of fossils in the "Chouteau" is better understood, the discord will fade away.

REFERENCES

BRANSON, E. B., and others, 1938, Stratigraphy and paleontology of the Lower Mississippian of Missouri: Univer. Missouri Studies, vol. 13, nos. 3 and 4, pp. 1–208, figs. 1–12, 15–18, pls. 1–48.

CLARK, E. L., and BEVERIDGE, T. R., 1952, A revision of the early Mississippian nomenclature in western Missouri: pp. 71–79, figs. 1–3; In Guidebook, 16th Regional Field Conference, Kansas Geol. Soc., pp. 1–93.

EASTON, W. H., and GUTSCHICK, R. C., 1953 (in press), Corals from the Redwall limestone (Mississippian) of Arizona: Bull. So. Calif.

Acad. Sci., vol. 51, pt. 1, pp. 1–33, text figs. 1–7, pls. 1–2.

LAUDON, L. R., and BOWSHER, A. L., 1949, Mississippian formations of southwestern New Mexico: Geol. Soc. America, Bull, vol. 60, pp. 1–88.

SPRENG, A. C., 1952, West central and southwestern Missouri, 16th Regional Field Conf., Guide Book, Kansas Geol., Soc., pp. 81–86.

STOYANOW, A. A., 1938, Correlation of Arizona Paleozoic formations: Geol. Soc. America, Bull., vol. 47, pp. 459–540.

WACHSMUTH, C., and SPRINGER, F., 1897, North American Crinoidea Camerata: Harvard Univ., Mus. Comp. Zool., Mem., vol. 20–21, pp. 1–837.

A METHOD OF SELECTING SAMPLE SIZES

MARVIN L. SMITH
Shell Oil Company, San Antonio, Texas

In zonal studies of microfossils, when the objective includes quantitative data on the numbers of specimens as well as qualitative data regarding the species present, micropaleontologists frequently are confronted with the problem of selecting the smallest sample that will contain a representative fauna. The writer presents here a method employed by him in a study of the ostracodes of the Middle Devonian Ludlowville shales of Western New York, for a master's thesis at the University of Rochester. In many outcrops these shales are sufficiently weathered so that the ostracodes readily can be washed free of the disintegrated matrix.

In collecting material for this study it was decided that each sample should, as closely as possible, represent a five-foot sequence of beds. To determine the minimum quantity of washed residue to be examined, it was necessary to obtain samples from some horizons that were quite fossiliferous and from others that were only sparingly so. Five large grab samples (750 cc. for convenient size) representing this extreme variation in fossil content were secured and washed leaving a residue of macrofossil fragments, microfossils, and small pieces of shale. These residues were sieved with an 18-mesh screen to remove the larger shale and macrofossil fragments.

Two common means of standardizing the amount of washed residue to be used in this type of study are by using arbitrarily selected weights or by arbitrarily selected volumes of material. A preliminary examination of several samples indicated that standardization could not be affected by the determination of an ideal weight as many of these samples contained great quantities of marcasite while others contained none at all. In the samples where much marcasite was present the amount of residue to be examined (determined on a weight basis) would be much less than in the marcasite-poor samples. This difference in amounts of residue examined would give a false impression of the relative number of fossils present from one sample to another.

The selection of a standard volume of residue then appeared to be the more practical means of sample comparison. From each of the five prepared grab samples five subsamples of graded size were measured (1.6 cc., 3.25 cc., 5 cc., 6.75 cc., and 8.5 cc.). Each of the subsamples from all five grab samples were examined with a binocular microscope, and all identifiable ostracodes and fragments were counted and the numbers recorded. On a graph (fig. 1A) the total number of species was plotted on the ordinate and the volume on the abscissa. As was to be expected the curve leveled off when no additional species were observed in the progressively larger samples. In this particular instance the curves for all five samples leveled off at the same size (5 cc.).

As a check on the adequacy of the 5 cc. sample to yield a quantitatively accurate picture of the relative number of specimens of different species present, as well as the number of species, the ratio of the number of specimens of two species common to samples of all sizes. (*Quasillites lobatus* Swartz and Oriel, 1948, and *Ponderodictya bispinulata* [Stewart, 1927]) was plotted against sample size (fig. 1B). The ratio of the number of specimens was found to remain constant above the 3.25 cc. sample

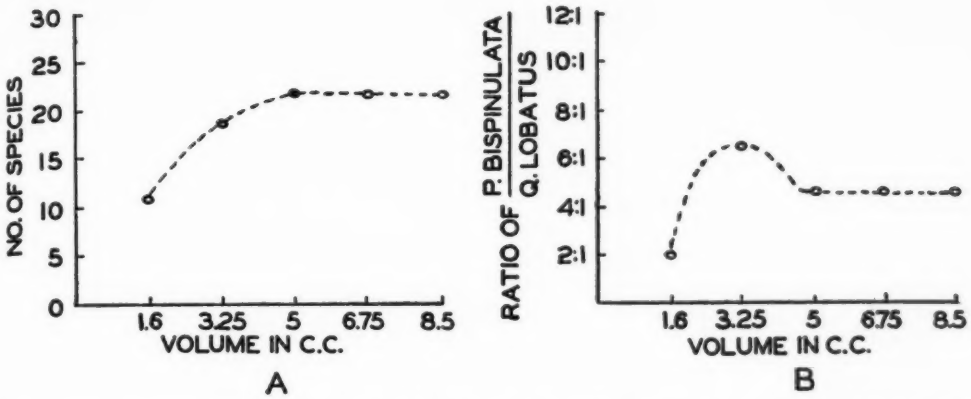


FIG. 1. A—The total number of species is plotted on the ordinate and the volume on the abscissa B—The ratio of *Ponderodictya bispinulata* (Stewart, 1927) to *Quasillites lobatus* Swartz and Oriel 1948 is plotted on the ordinate against the sample size on the abscissa.

size (see fig. 1B). The 5 cc. volume was then selected as the standard measure of prepared residue to be examined from each five foot sample.

It is realized that samples taken from other formations may not yield such regular results as in this case where the quantity of residue is the same for the poorly fossiliferous samples as for the very fossiliferous samples. However, it is felt that the procedures outlined above for determining minimum sample size and for checking its adequacy should prove generally applicable.

Grateful appreciation is expressed to Dr. William R. Evitt of the University of Rochester for critically reading the manuscript.

A PERMIAN *ANCISTRUM* (HOLOTHUROIDEA) FROM KANSAS

LOUIS S. KORNICKER
Columbia University

INTRODUCTION

A single holothurian spicule of the genus *Ancistrum* was found in the Permian Florena shale of Kansas. The specimen is the first reported occurrence of the genus from the Permian of North America.

The author wishes to thank Dr. J. Imbrie who collected the material in which the spicule was found for his helpful suggestions and advice.

The sample was taken from the bottom 12 inches of the Florena shale member of the Council Grove group, Wolfcampian series, at a roadcut 4 miles southeast of Manhattan, in the northeast quarter of section 34, T. 10 S., R. 8 E., Riley County, Kansas.

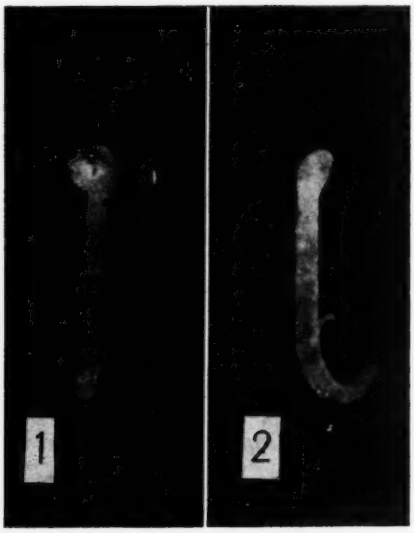
Collection of the sample was sponsored by the State Geological Survey of Kansas.

SYSTEMATIC DESCRIPTION

ANCISTRUM BROWNWOODENSIS Croneis
Figures 1, 2

Ancistrum brownwoodensis CRONEIS, 1932, Jour. Paleontology, vol. 6, p. 143, pl. 21, figs. 3–8, 19–22, 29, 39.

Spicule gives impression of fishhook lacking barbed tip. Haft straight in section between hook and eye. Eye inclined slightly in general direction of hook projection. Plane of hook and haft forms slight angle with plane of eye giving a complicated twist to spicule. Eye hole diameter smaller than diameter of haft. The dimensions of the only Permian specimen found are:



FIGS. *1, 2*—*Ancistrum brownwoodensis* Croneis, ×45.

Measurements of Ancistrum brownwoodensis

	mm.
Length	0.75
Greatest diameter of haft	0.075
Greatest length of point	0.117
Width of hooked portion	0.25
Inside diameter of eye (approximate)	0.033
Outside diameter of eye	0.15

Remarks.—This species differs from *A. permianum* (Spandel) in having a straighter haft and inclined eye.

Collection.—Columbia University, on loan from University of Kansas.

REFERENCES

CRONEIS, C., and MCCORMACK, J., 1932, Fossil Holothuroidea: Jour. Paleontology, vol. 6, p. 131, pl. 19, figs. 25–27, 30?, p. 143, pl. 21, figs. 3–8, 19–22, 29, 39.

SPANDEL, E., 1898, Die Echinodermen des deutschen Zechsteins: Naturhist. Gesell. Nürnberg, Abhandlungen, 11, pp. 17–45.

RHOPALONARIA LAMBTONENSIS, N. SP.

MADELEINE A. FRITZ
Royal Ontario Museum of Zoology and Palaeontology, Toronto, Canada

Description.—A stoloniferous growth, slightly pinnate to radiate, forming a semi-reticulate incrustation on the under surface of a specimen of *Microcyclus discus* Meek and Worthen. Connecting stolons delicately filiform; in general stolons two or three (or even more) times longer than the internodes. Internodes vary in shape and size from delicate fusiform segments 0.3 mm. long with a diameter of 0.1 mm. or less, to ovate, bulbous structures approximately 0.15 mm. long with an almost equal diameter. All the zoarial elements are in the form of casts rather than the usual excavations common to the genus. Owing to this circumstance, and in that the stolons are very slender, the internodes stand out in relatively bold relief; no pores are visible, on the internodes.

Remarks.—*Rhopalonaria lambtonensis* finds its closest relative in *R. attenuata* Ulrich and Bassler from the Lockport, Middle Silurian. These two species show a marked resemblance in the size and general character of the various zoarial elements. The characteristic pinnate arrangement of *R. attenuata* is, however, less developed in the new species which also shows more variation

FIG. *1*—*Rhopalonaria lambtonensis* Fritz, n. sp., ×5.

in the shape of the internodes. From the associated Middle Devonian *R. tenuis* Ulrich and Bassler, the present species is distinguished by its longer and more delicate connecting stolons and the smaller size of the internodes, which are more variable in shape than in *R. tenuis*, in which species they are strictly fusiform.

Of the various examples of *Rhopalonaria* in the Museum collections only one appears to conform to the above description.

Holotype.—No. 27119, Royal Ontario Museum of Zoology and Palaeontology collection.

Occurrence.—Hamilton, Middle Devonian, Thedford, Ontario.

PRESBYNILEUS AND *PROTOPRESBYNILEUS*, NEW GENERIC NAMES PROPOSED FOR *PSEUDONILEUS* AND *PARANILEUS* HINTZE, PREOCCUPIED

LEHI F. HINTZE
Oregon State College, Corvallis

Professors Chr. Poulsen, Alois Pribyl, and T. Kobayashi have kindly informed me that two names, *Paranileus* and *Pseudonileus*, proposed for new trilobite genera by me (1952, p. 196, 223) have been used previously by Kobayashi (1951, p. 41) for two Bohemian nileid trilobites. Accordingly, I propose the name *Presbynileus* as a substitute for *Paranileus* Hintze 1952—non Kobayashi 1951, with *P. ibexensis* Hintze as the genotype; and *Protopresbynileus* as a replacement for *Pseudonileus* Hintze 1952—non Kobayashi 1951, with *P. willdeni* Hintze as the genotype.

REFERENCES

HINTZE, L. F., 1952, Lower Ordovician trilobites from western Utah and eastern Nevada: Utah Geol. Min. Survey, Bull. 48, 249 pp., 28 pls. First distributed in February, 1953.

KOBAYASHI, T., 1951, Ordovician trilobites in central China: Journ. Fac. Sci., Univ. of Tokyo, section 2, vol. 8, pt. 1, pp. 1–87, 5 pls.

CORRECTION

J. C. WALTER, JR.

Regrettably, certain correspondence from J. Brookes Knight was credited to Norman Newell in a recent publication, "Paleontology of the Rustler Formation, Culberson County, Texas," JOUR. PALEONTOLOGY, vol. 27, no. 5. On page 687 I wrote, "With the exception of *Euphemites circumcostatus* Walter nl sp., which may be significant of the young age, the gastropods are not particularly diagnostic (Newell, written communication)." This correspondence was actually received from J. Brookes Knight. My apologies to Dr. Knight and Professor Newell for this unfortunate misquotation.

On page 697 in the explanation of Plate 73, fig. 6 was reported to be *Plagioglypta annulistriata* (Meek and Worthen). Fig. 6 is actually *Streptacis?* cf. *S. permiana* (Beede) Knight.

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 1, P. 120, JANUARY 1954

SOCIETY RECORDS AND ACTIVITIES

NOMINATIONS FOR OFFICES IN THE PALEONTOLOGICAL SOCIETY FOR 1954–55

In accordance with the provisions of Chapter III, Section 2 of the By-Laws, the Council of the Paleontological Society announces the following nominations for the offices of the Society for 1954–55:

For President: A. SCOTT WARTHIN, JR., Poughkeepsie, N. Y.
For Vice-President: V. J. OKULITCH, Vancouver, British Columbia
For Treasurer: FRANK M. SWARTZ, State College, Pa.
For Editor: WM. R. EVITT, II, Rochester, N. Y.
For Secretary: K. E. CASTER, Cincinnati, Ohio.

Chapter III, Section 2 of the By-Laws provides that "Any twenty members may forward to the Secretary of the Society other nominations for any or all offices. All such nominations reaching the Secretary at least sixty days before the Annual Meeting shall be printed, together with the names of the nominators, as special tickets."

NOMINATIONS FOR MEMBERSHIP

In accordance with Art. 3, Chap. 1, of the By-Laws, the Secretary submits the following nominations for membership in the Paleontological Society. The list has been approved by the Council of the Society.

AMSBURY, DAVID L., Box 7907, University Sta., Austin 12, Texas. K. Young, S. P. Ellison Jr., John A. Wilson.

BANKS, MAXWELL ROBERT, Geol. Dept., Univ. Tasmania, Hobart, Tasmania. K. G. Brill, Jr., K. E. Caster.

BROWN, NOEL KING, JR., Cuban Gulf Oil Co., Aplado 729, Habana, Cuba. P. Bronniman, K. E. Caster.

CHAFFEE, ROBERT G., Dartmouth College Museum, Hanover, N. H. A. S. Warthin Jr., K. E. Caster.

COPELAND, MURRAY JOHN, 10 Glenmount Pk. Rd., Toronto 13, Canada. E. C. Stumm, L. B. Kellum, G. M. Ehlers.

DIAZ, JOSE CORVALAN, Dept. Paleontology, Univ. California, Berkeley 4, Calif. J. W. Durham, J. H. Peck, Jr.

DORECK, HERTHA SIEVERTS-, Stuttgart-Degerloch Figarostr. 5, Württemberg, Germany. K. E. Caster, R. C. Moore.

DUAHE, JOHN W., 807 S. State, Ann Arbor, Mich. E. C. Stumm, G. M. Ehlers, C. W. Hibbard.

GLOVER, LYNN, III, Box 6147, University, Ala. Byron N. Cooper, Wayne E. Moore.

GOMEZ, JOSE ROYO Y, Aptdo. 4585-Este, Caracas, Venezuela. K. E. Caster, G. Botero-A.

GRAFFHAM, ALBERT ALLEN, Tucker Tower Museum, Box 419, Ardmore, Okla. R. L. Casanova, M. K. Elias.

HEWITT, PHILIP COOPER, Geol. Dept., Univ. Tennessee, Knoxville, Tenn. H. K. Brooks, P. B. Stockdale, F. D. Holland, Jr.

HOPKINS, ARTHUR H., 741 Beacon Lane, Merion, Pa. F. D. Holland, Jr., J. B. Pogue, II, K. E. Caster.

HOPPINGER, JOHN J., 11720 Edgewater Dr., Lakewood 7, Ohio. K. E. Caster, R. L. Casanova, F. D. Holland, Jr.

HORNADAY, GORDON RAYMER, Dept. Paleontology, Univ. California, Berkeley 4, Calif. R. M. Kleinpell, J. W. Durham, W. K. Emerson.

JAEKEL, JULIA ANNE, 715 Park Ave., New York 21, N. Y. J. Braunstein, W. M. Furnish, M. G. Mehl.

LOWTHER, J. STEWART, Mus. Paleontology, Univ. Michigan, Ann Arbor, Mich. C. A. Arnold, G. M. Ehlers, E. C. Stumm.

MARTIN, WAYNE M., Geol. Dept., Miami University, Oxford, Ohio. K. E. Caster, W. H. Shideler, F. D. Holland, Jr.

MCLAUGHLIN, ROBERT EVERETT, Dept. Botany, Univ. Tennessee, Knoxville, Tenn. H. K. Brooks, P. B. Stockdale, K. E. Caster.

PRICE, DON CLAUDE, 880 Cranbrook Rd., Birmingham, Mich. E. C. Stumm, C. W. Hibbard.

PURI, HARBANS S., Drawer 631, Tallahassee, Florida, G. E. Murray, A. S. Warthin, Jr.

RAYMOND, RICHARD HOWARD, Dept. Geol., Univ. Tennessee, Knoxville, Tenn. H. K. Brooks, P. B. Stockdale, K. E. Caster.

ROSS, MARY HARVEY, 405 Turner St., Blacksburg, Va. W. E. Moore, B. N. Cooper.

RUSSELL, ERNEST EVERETT, Dept. Geol., Univ. Tennessee, Knoxville, Tenn. H. K. Brooks, P. B. Stockdale, K. E. Caster.

SCHMIDT, HERMAN, Planckstr. 6, Göttingen, Germany. K. E. Caster, F. D. Holland, Jr.

STEHLI, FRANCIS G., 255 Stanton St., Pasadena, Calif. N. D. Newell, M. C. Israelsky, H. A. Lowenstam.

WAGNER, PHILIP L., 207 Wenley House, West Quad., Ann Arbor, Mich. E. C. Stumm, R. V. Kesling.

WALL, JOHN HALLETT, Box 1300, St. Stephen, N. B., Canada. R. E. Peck, A. G. Unklesbay.

ZINGULA, RICHARD PAUL, Sch. Geol., Louisiana State Univ., Baton Rouge 3, La. G. E. Murray, H. V. Howe.

ZOERKLER, RAYMOND NORBERT, Unit 23, Veterans Homes, Campus, Univ. Cincinnati, Cincinnati 21, Ohio. F. D. Holland, Jr., J. B. Pogue, II, K. E. Caster.

OFFICERS OF THE SOCIETIES

THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS

For the year ending March 1954

President, H. N. Fisk, Humble Oil and Refining Company, Houston, Tex.

Secretary-Treasurer, S. P. Ellison, Jr., University of Texas, Austin, Tex.

Editors

Grover E. Murray Baton Rouge, La., for paleontology.

W. H. Twenhofel, Orlando, Fla. (consulting editor) for mineralogy.

Jack L. Hough, Urbana, Ill. (editor) for mineralogy.

THE AMERICAN ASSOCIATION OF PETROLEUM GEOLOGISTS

For the year ending March 1954

President, John Emery Adams, Midland, Tex.

Past-President, Morgan J. Davis, Houston, Tex.

Vice-President, L. M. Clark, Calgary, Alberta, Can.

Secretary-Treasurer, E. H. Powers, Fort Worth, Tex.

Editor, A. J. Eardley, *Editor*, Salt Lake City, Utah.

THE PALEONTOLOGICAL SOCIETY

for the year ending November 1954

President, Harry S. Ladd, Washington, D. C.

Vice-President, George M. Ehlers, Ann Arbor, Mich.

Secretary, Kenneth E. Caster, Cincinnati, O.

Treasurer, Frank M. Swartz, State College, Pa.

Editor, William R. Evitt, Rochester, N. Y.

Chairman, Pacific Coast Section, A. A. Stoyanow, Tucson, Ariz.

Ex-Presidents

Harold E. Vokes, Baltimore, Md., 1951.
Julia A. Gardner, Washington, D. C., 1952
W. Storrs Cole, Ithaca, N. Y., 1953

JOINT COMMITTEE ON ZOOLOGICAL NOMENCLATURE FOR PALEONTOLOGY IN AMERICA

Sponsored by the Society of Economic Paleontologists and Mineralogists, The Paleontological Society, and the Society of Vertebrate Paleontology in support of the International Commission on Zoological Nomenclature.

Policy Board

G. Winston Sinclair, *Chairman* (PS)
R. C. Moore (PS), Bryan Patterson (SVP)

Members

Raymond C. Moore J. Brookes Knight G. Winston Sinclair John W. Wells	1951–1953
S. W. Muller J. B. Reeside, Jr. Bobb Schaefer J. M. Weller	1952–1954

Address all communications to the chairman. G. Winston Sinclair, Ohio Wesleyan University, Delaware, O.

THE GEOLOGICAL SOCIETY OF AMERICA

For the year ending November 1954

President, Ernst Cloos, Baltimore 18, Md.

Past President, Wendell P. Woodring

Vice-Presidents: Walter H. Bucher; John G. Bartram; W. Storrs Cole; Joseph D. H. Donnay

Secretary, H. R. Aldrich, New York, N. Y.

Treasurer, J. Edward Hoffmeister, Rochester, N. Y.

Councillors

Glenn L. Jepsen Philip B. King Harrison Schmitt	1952–1954
Arthur A. Baker Ian Campbell Edwin D. McKee	1953–1955
Hollis D. Hedberg James E. Gill Philip J. Shenon	1954–1956

THE McLEAN CARD CATALOGUE OF AMERICAN FORAMINIFERA

Species cards of important forms of Foraminifera useful in research and in commercial stratigraphic work, comprising the description, illustrations and source of each given species.

Volumes I, II, III and a cumulative index to the three volumes (over 1,200 species cards) can now be had.*

Volume IV (the 1954 series) available by subscription.

*Due to unexpectedly large sales of certain units, a temporary shortage of parts of volumes I, II & III exists. A short delay in delivery of certain units may be expected until printing schedules are met to replace these temporarily exhausted supplies.

The Cumulative Index and full details are available without charge to persons requesting information. Write to:

James D. McLean, Jr., P.O. Box 916, Alexandria, Virginia, U.S.A.